1-1-2009

Distribution of Woodland Salamanders of the Valley and Ridge in West Virginia

H. Reid Downer

Distribution of Woodland Salamanders of the Valley and Ridge in West Virginia

Thesis submitted to
the Graduate College of
Marshall University

In partial fulfillment of the
requirements for the degree of
Master of Science
Biological Sciences

by

H. Reid Downer

Thomas K. Pauley, Committee Chair
Jayme L. Waldron, Committee Member
Dan K. Evans, Committee Member

Marshall University

May 2009

ABSTRACT

Distribution of Woodland Salamanders of the Valley and Ridge in West Virginia

H. REID DOWNER. Department of Biological Sciences, Marshall University, One John Marshall Drive, Huntington, WV 25755
Email: downer@marshall.edu

Two terrestrial woodland salamanders of the genus *Plethodon*, *P. punctatus* and *P. virginia*, are endemic to the Valley and Ridge Physiographic Province in West Virginia and Virginia and occupy limited geographic ranges. Two common and widespread species, *P. cylindraceus* and *P. cinereus*, also inhabit this region. To evaluate the distribution and habitat of these terrestrial salamanders I surveyed wooded ridges and slopes throughout the geographic range of the two endemic species by conducting daytime cover object searches and nocturnal visual encounter surveys. From March through November 2008, I recorded the presence of 321 woodland salamanders at 91 sites. I used two types of modeling to evaluate the distributions of these species with site occupancy data. I used logistic regression to evaluate *a priori* models that were developed with presence-absence data and associated environmental variables from 2008 surveys and ranked them with Akaike's Information Criterion corrected for small sample size (AIC_c). I then used historic and current presence data to model the distribution of each species with the software program Maxent with WorldClim climatic variables. Logistic regression models revealed that *P. punctatus* and *P. cinereus* had positive associations with elevation, *P. virginia* was negatively associated with relative humidity, and *P. cylindraceus* occurrence was negatively associated with elevation and positively associated with ambient temperature and relative humidity. Maxent distribution models were evaluated and suggested that the distributions of woodland salamanders are likely shaped by both climatic factors as well as biological factors, possibly in the form of competition. These results suggest that *P. punctatus* is associated with rocky substrates primarily among or near talus at high elevations. *Plethodon virginia* inhabits relatively dry ridges and slopes at all elevations. *Plethodon cylindraceus* is widespread throughout habitat types at lower elevations, while *P. cinereus* is largely limited to mesic habitats in this region.

ACKNOWLEDGEMENTS

I would first like to thank my advisor, Dr. Thomas Pauley, for the opportunity to be a part of the Marshall herpetology lab. It was a great pleasure to work with and learn from Dr. Pauley, whose great depth of knowledge and experience in the field of herpetology, especially in West Virginia, was invaluable to this project. I have a great deal of respect admiration for Dr. Pauley for the extensive work that he does for conservation, for being a great teacher, and for being such a pleasant person to interact with on all levels.

I was very fortunate to have had advice and help from Dr. Jayme Waldron, who came to the lab in Fall 2008 and essentially became my second advisor and served on my graduate committee. This thesis benefited greatly from the time she spent with me on statistics and modeling. I am very grateful to her for introducing and teaching me those tools, and for being so willing to help me with any questions and problems that arose.

I would also like to thank Dr. Dan Evans who served on my graduate committee and was my plant taxonomy professor for two semesters. I appreciate his helpful suggestions and comments on my thesis. My knowledge of botany and systematics, and my ability to identify plants have grown a great deal as a result of his classes. I am fortunate to have had the chance to benefit from his expertise.

I am very grateful to several friends and colleagues who contributed greatly to this project. I had help in the field from Casey Bartkus, Scott Jones, Warren McLellan, Chris Chamberlin, Ryan Farr, Jeff Pool, Steven Silverstein, and Cameron Bartkus. Their time, energy, and company provided material support to this research and helped make it a more enjoyable experience. Adam Fannin, Scott Jones, and Casey Bartkus helped me develop maps with GIS software. Thanks to Warren McLellan and Chris Chamberlin for providing a place to stay that was closer to the eastern panhandle than Huntington, which saved me much gas and time. Thanks to Billy Flint, who provided helpful advice on surveying for *Plethodon punctatus*, and Matt Graham, a former member of the Marshall herpetology lab, who also provided helpful advice on *Plethodon punctatus* as well as species distribution modeling.

The Division of Amphibians and Reptiles, National Museum of Natural History provided historical site locality data. Thanks especially to Addison Wynn, who kindly provided this data in a convenient format.

Thanks to the West Virginia Department of Natural Resources (WVDNR) and the Marshall University Graduate College for funding. Thanks to the U.S. Forest Service (USFS) and the George Washington National Forest for permitting me to conduct surveys on USFS land. The WVDNR and the Virginia Department of Game and Inland Fisheries (VADGIF) issued scientific collection permits to collect data on animals in the field: WVDNR Permit Number 2008.090; VADGIF Permit Number 033681. This research was reviewed and approved by the Marshall University Institutional Animal Care and Use Committee (IACUC): IACUC Project Number 385.

Finally, I would like to thank my parents for all of their love and support.

TABLE OF CONTENTS

LIST OF FIGURES

Figure Page

All photographs by H. Reid Downer

LIST OF TABLES

Table Page

CHAPTER ONE

Introduction and Species Accounts

There are 55 recognized species of salamanders in the genus *Plethodon* (Family: Plethodontidae), the woodland salamanders (Frost 2009). These salamanders, which are found only in North America, are completely terrestrial, and do not require an aquatic habitat because their larval stage is completed entirely inside the egg. Young emerge from eggs as juveniles that resemble miniature adults (Conant & Collins 1998). Because plethodontid salamanders are lungless and breathe cutaneously, they require moist microhabitats to avoid desiccation (Duellman & Trueb 1986). Woodland salamanders use cover objects such as rocks, logs, rock crevices, and leaf litter on the forest floor to keep their skin and eggs moist. Deeper underground burrows and rock crevices may be used during dry spells, over-wintering, and for brooding (Petranka 1998; Conant & Collins 1998). Woodland salamanders are generally nocturnal, and because relative humidity is higher at night, they emerge from cover objects to mate or forage for small invertebrates especially in nighttime wet conditions (Petranka 1998), but they are occasionally active during the day (Highton 1995). In Eastern North America, woodland salamanders are divided into two major groups, the large *Plethodon*, and the small *Plethodon*. The small *Plethodon* have bodies that are generally more slender and elongate, while the large *Plethodon* are proportionately more robust, and more massive (Grobman 1944; Highton 1972).

The genus *Plethodon* is most diverse in the Appalachians (Duellman & Sweet 1999), and is distributed throughout the entire state of West Virginia (Green & Pauley

1987). The Valley and Ridge Physiographic Province, which passes through the eastern panhandle of West Virginia, represents a relatively hot and dry region within the Appalachians, and is the hottest and driest physiographic province in West Virginia (Strausbaugh & Core 1978). Two endemic species of the genus *Plethodon* inhabit the Valley and Ridge Physiographic Province in West Virginia. This study focuses within the ranges of these two endemic species, *Plethodon punctatus* (Cow Knob Salamander, Figure 1) and *Plethodon virginia* (Shenandoah Mountain Salamander, Figure 2). *Plethodon virginia* is limited to Pendleton, Hardy, Grant, and Hampshire counties, West Virginia, and western Rockingham County, Virginia. *Plethodon punctatus* is found in Pendleton, Hardy and Hampshire counties, WV and Augusta, Highland, Rockingham, and Shenandoah counties, VA. The two remaining *Plethodon* species that inhabit this range, *P. cinereus* (Eastern Red-backed Salamander, Figure 3) and *P. cylindraceus* (White-spotted Slimy Salamander, Figure 4) are more common and have widespread distributions (Lannoo 2005).

Plethodon punctatus (Highton 1972)

Cow Knob Salamander

Plethodon punctatus is a large eastern *Plethodon* of the *P. wehrlei* species group that reaches snout-vent length (SVL) of about 75 mm (Flint 2004), a total length that ranges from 100-170 mm, and mass of up to just over 5 g. The dorsum is brown to black with irregular cream-colored spots. The underside is uniformly dark gray, with a light-colored throat (Green & Pauley 1987). *Plethodon punctatus* is a sibling species of the more common and widespread *P. wehrlei* (Wehrle's Salamander), which is common in the

Allegheny Mountain Province. *Plethodon wehrlei* is a dark gray to black salamander with lateral whitish blotching. The dorsum is often speckled with tiny white flecks. Juvenile *P. wehrlei* sometimes have irregular orange spots that occur in pairs along the dorsum, which *P. punctatus* lack. According to Highton (1972), *P. punctatus* have 17 to 18 costal grooves, while *P. wehrlei* usually have 17 costal grooves. *Plethodon punctatus* also superficially resemble slimy salamanders (*Plethodon glutinosus* complex), but are typically smaller, have highly webbed feet, and have more costal grooves.

The known distribution of *P. punctatus* reaches north from Nathaniel Mountain in southern Hampshire County, WV south to Hardscrabble Knob on Shenandoah Mountain in Augusta County, VA (Highton 1972; Pauley 1998; Flint 2004; Graham 2007). Most sites are located on Shenandoah Mountain, while disjunct populations have been recorded on Jack Mountain to the west (Graham 2007), Nathaniel Mountain to the north and Great North Mountain to the east (Highton 1972). The distribution of *P. punctatus* is restricted to relatively high elevations on mostly north-facing slopes (Buhlmann et al. 1988; Pauley 1995). Most sites are located above 950 m, but populations have been found down to 732 m (Mitchell and Pauley 2005). Buhlmann et al. (1988) found that *P. punctatus* was associated with rocky substrates in relatively undisturbed forest habitats on Shenandoah Mountain in Virginia. They suggested that rocky substrates with thin soil might have provided some degree of refuge from logging operations and fire, which was common before the U.S. government purchased the George Washington National Forest between 1911 and 1940 (Buhlmann et al. 1988). Much of the known range of *P. punctatus* on Shenandoah Mountain is now located within the George Washington National Forest.

Because *P. punctatus* is restricted to high elevations along a narrow and limited range that extends beyond Shenandoah Mountain only by a few disjunct populations, it is a species that is of particular conservation concern. The West Virginia Division of Natural Resources (WVDNR) currently lists *P. punctatus* as an S1 species, which is defined as extremely rare and critically imperiled, while in Virginia, *P. punctatus* is listed as an S2 species (very rare and imperiled) by the Virginia Department of Natural Heritage (VDNH). Globally, *P. punctatus* is listed as Near Threatened on the International Union for the Conservation of Nature (IUCN) Red List (www.iucnredlist.org), and is listed as a G3 (vulnerable) species by NatureServe (www.natureserve.org) due to a small range, high local abundance, and vulnerability to deforestation.

Highton first described *P. punctatus* in 1972 after observing geographically isolated populations with subtle morphological and distinct color pattern differences from typical *Plethodon wehrlei* populations from the Allegheny Plateau. An electrophoretic protein comparison indicated that *P. punctatus* and *P. wehrlei* were two distinct but closely related species based on the observed Nei's genetic distance (D = 0.18), though the difference was on the threshold of the level of genetic distance generally attributed to separate species within the genus *Plethodon* (Highton & Larson 1979; Highton 1990, 1995). Since it was described, *P. punctatus* has been generally accepted as a distinct species by taxonomists and herpetologists (Green & Pauley 1987; Conant & Collins 1998; Petranka 1998; Crother et al. 2001; Mitchell & Pauley 2005), though some have questioned the use of seemingly arbitrary genetic distances to delimit species (Frost and Hillis 1990).

Plethodon virginia (Highton, 1999)

Shenandoah Mountain Salamander

Plethodon virginia is a small eastern *Plethodon* in the *P. cinereus* species group that grows to about 55-60 mm SVL, and ranges from 80-130 mm total length and a mass of about 2.0-2.5 g. The dorsum is black laterally with an indistinct medial brown stripe and is speckled dorsally and laterally with abundant white flecks. The indistinct brown stripe is sometimes infused with blotches of reddish pigmentation. The belly is dark with abundant white flecks, and the chin is light-colored with numerous white blotches. Tail length of adult *P. virginia*, when tails are un-broken, are usually longer than body length. *Plethodon virginia* is superficially indistinguishable from its sibling species, *P. hoffmani*, the Valley and Ridge Salamander (Highton 1999). The lead-back phase of *Plethodon cinereus* is also superficially similar to *P. virginia*, but the ventral surface contains more white spots that are generally larger and form irregular blotches rather than small flecks. However, this characteristic tends to vary among populations within both species and therefore is not always reliable (Highton 1999). *Plethodon virginia* and *P. hoffmani* are generally longer, have proportionally longer tails, more trunk vertebrae (and therefore more costal grooves), and in adults appear to be more elongated than *P. cinereus*. Highton and Jones (1965) described a population *of P. virginia* on Shenandoah Mountain near Reddish Knob in Rockingham County, VA that included individuals with a red dorsal stripe. The striped individuals were distinguishable from *P. cinereus* in that *P. virginia* specimens had more trunk vertebrae and a narrower dorsal stripe that did not extend to the tail as in *P. cinereus*.

The range of *P. virginia* extends from central Hampshire County, WV south to central Pendleton County, WV and western Rockingham County, VA. The northern and southern limits of the range of *P. virginia* overlap with the range of *P. hoffmani* where zones of hybridization have been identified (Highton 1999). Highton (1999) suggested that the South Branch of the Potomac River is the likely western boundary of *P. virginia*. Within its range, *P. virginia* has been found from 536 to 1200 m elevation on forested slopes and ridges.

Plethodon virginia is listed as an S2 species in West Virginia and Virginia and G2G3Q globally (where Q denotes questionable taxonomy) by NatureServe and as Near Threatened by the IUCN. The IUCN currently describes the distribution of *P. virginia* as limited to elevations between 1100-1200 m above sea level, which is erroneous (the type specimen, however, was collected between 1100 and 1200 m elevation); the known elevational range of *P. virginia* is actually from 530-1200 m above sea level (Table 4; Figure 5). The reason for designation as imperiled and near threatened is due to a limited range and sites where the species has been recorded. Despite the erroneous elevations described by the IUCN, the range of *P. virginia* is endemic to only a narrow portion of the Valley and Ridge. No studies have focused on the ecology and natural history of *P. virginia* since its description in1999 when Highton split *P. virginia* from what is now considered its sibling species, *P. hoffmani* (Valley and Ridge Salamander). *Plethodon virginia* has been included in studies when it was still considered *P. hoffmani* prior to 1999 (Fraser 1976a,b) and *P. richmondi* before 1972 when *P. hoffmani* was initially described (Highton & Jones 1965).

Plethodon virginia was split from *P. hoffmani* based on allozyme data from electrophoretic protein comparisons in which the two species differed according to the resulting Nei's genetic distance of D = 0.21 (Highton 1999). Though this method of delimiting species has not always been accepted (Frost & Hillis 1990, see above), *P. virginia* has largely been treated as a separate species since its description (Crother et al. 2001; Beamer & Lannoo 2005; Wiens et al. 2006; Kozak & Wiens 2006; Kozak et al. 2006).

Plethodon cinereus (Green, 1818)

Eastern Red-backed Salamander

Plethodon cinereus is a small eastern *Plethodon* that is one of the most abundant, widely distributed, and widely studied salamanders within its genus. Most individuals have a dorsal straight red stripe that extends from the head to the tail. The lateral surfaces are dark with light-colored flecking. The venter is mottled with approximately equal amounts of black and white, and the area under the chin is mostly light-colored. Multiple color variations have been described, the most common of which is the lead-backed or unstriped morph, which lacks the dorsal red stripe and has a more uniformly dark dorsum, often with white and brassy flecking. Other less common morphs include an erythristic morph that is colored a uniform red dorsally and laterally (Pauley et al. 2001). Adults may reach a SVL of 45-50 mm, and range from 65-125 mm in total length (Petranka 1998).

The range of *P. cinereus* extends from southeastern Canada south to northern North Carolina and southern Indiana, and west to the eastern edge of Illinois, and eastern

Minnesota. The eastern boundary is the Atlantic Coast (Petranka 1998). *Plethodon cinereus* is distributed throughout West Virginia, with the exception of the Ohio Valley region (Green & Pauley 1987). Though *P. cinereus* is found within the Valley and Ridge in West Virginia, it is largely absent from the western two-thirds of the province, and only appears to occur in several isolated populations (Highton 1972; Fraser 1976b; Highton 1999). Within its range, *P. cinereus* is found at all elevations in woodland habitat and is often locally abundant (reviewed in Petranka 1998). *Plethodon cinereus* has been associated with relatively cool and mesic forest habitats and more negatively associated with comparatively hotter, drier climates (Highton 1972; Fraser 1976b; Pauley 1978). *Plethodon cinereus* is listed as secure (S5) in both West Virginia and Virginia, and globally (G5), and is only listed as vulnerable in Kentucky (S3), where *P. cinereus* is at the very edge of its range.

Plethodon cylindraceus (Harlan, 1825)

White-spotted Slimy Salamander

Plethodon cylindraceus is a large eastern *Plethodon* that belongs in the *P. glutinosus* species complex, which consists of 16 distinct species (Highton & MacGregor 1983; Highton 1989, 1995). *Plethodon cylindraceus* is a robust salamander that has a uniformly black ground color throughout its body with the exception of a white and light-gray mottled mental region that contrasts with a dark belly. Large irregular white blotches are abundant dorsally and laterally as well as on the legs, head, and anterior half of the tail. Adults reach up to about 200 mm (Green & Pauley 1987; Petranka 1998) and up to a mass of 13 g. In West Virginia, there are two other species within the *P.*

glutinosus complex: *P. glutinosus* (Northern Slimy Salamander) and *P. kentucki* (Cumberland Plateau Salamander), which are similar to *P. cylindraceus*. The range of *P. kentucki* extends only to the southwestern West Virginia in the Cumberland Plateau region of the Appalachian Plateau (Green & Pauley 1987). *Plethodon glutinosus* and *P. cylindraceus* have a parapatric contact zone from Maryland to Tennessee, which extends through the Valley and Ridge in West Virginia, and hybrid zones have been recorded in Maryland and Virginia (Highton 1989; Highton & Peabody 2000). *Plethodon glutinosus* has dorsal and lateral spots that are more brassy-to-yellow rather than white and has a mental region that is dark-colored and uniform with the color of the ventral surface (Highton 1989).

The range of *P. cylindraceus* extends from the West Virginia panhandle and Northern Virginia south to the Piedmont of central South Carolina, west to the French Broad River and the Blue Ridge Physiographic Province in eastern North Carolina and Tennessee and the Potomac River in the Valley and Ridge in West Virginia and Virginia, and east to the Costal Plain of eastern Virginia (Highton 1989). In West Virginia, *P. cylindraceus* is found in the Valley and Ridge in Pendleton, Hardy, Grant and Hampshire counties. Highton and Peabody (2000) described a population where *P. cylindraceus* hybridizes with *P. glutinosus* in Washington County, Maryland, but there is no further information to suggest that *P. cylindraceus* is a separate and valid species in Maryland. Within its range in West Virginia, *P. cylindraceus* inhabits woodlands from the lowest to highest elevations, but is more common at lower elevations. Because Highton's (1995) taxonomy of the *P. glutinosus* group has not been uniformly accepted, and has been treated ambiguously by Petranka (1998) and Conant and Collins (1998), listing of separate species within this species group by government and conservation organizations (e.g., NatureServe) is also not uniform. NatureServe does not recognize *P. cylindraceus* as a species and lists *P. glutinosus* as globally secure, and suggests that if each species within the complex were recognized, a G5 listing would still be warranted. The Integrated Taxonomic Information System (ITIS), a federal interagency organization, considers *P. cylindraceus* a valid species (www.ITIS.gov). Regardless of its taxonomy, neither *P. glutinosus* nor *P. cylindraceus* is listed as species of concern in any state, and the IUCN, which recognizes *P. cylindraceus* as a valid species, lists it as a species of Least Concern due to its wide distribution and presumed large populations. Crother et al. (2000), Weisrock et al. (2005), and Frost (2009) also recognize *P. cylindraceus* as a valid species.

Figure 1. *Plethodon punctatus*, Hardy County, WV, November 2008.

Figure 2. *Plethodon virginia*, Pendleton County, WV, November 2008.

Figure 3. *Plethodon cinereus*, Hardy County, WV, October 2008.

Figure 4. *Plethodon cylindraceus*, Pendleton County, WV, May 2008.

CHAPTER TWO

The Distribution of the genus *Plethodon* in the Valley and Ridge of West Virginia

Abstract

The distribution of terrestrial woodland salamanders of the genus *Plethodon* has been the subject of several studies that have illustrated non-random patterns of co-occurrence and ranges that are likely shaped by interspecific interactions, climate, and topography. The seemingly continuous expansion of the genus resulting from the recognition of cryptic species following genetic studies has created the need to evaluate the distributions of these species. Two of these salamanders, *P. punctatus* and *P. virginia*, are endemic to the Valley and Ridge Physiographic Province in West Virginia and Virginia and occupy limited geographic ranges. Two common and widespread species, *P. cylindraceus* and *P. cinereus*, also inhabit this region. I investigated the distribution and habitat of these terrestrial salamanders by surveying wooded ridges and slopes throughout the geographic range of the two endemic species. I surveyed for salamanders by conducting daytime cover object searches and nocturnal visual encounter surveys. I recorded geographic locations with a GPS receiver and recorded environmental data including relative humidity, ambient temperature, soil temperature, substrate type, and elevation. From March through November 2008, I recorded the presence of 321 woodland salamanders at 91 sites, including 74 *P. punctatus* at 23 sites, 48 *P. virginia* at 33 sites, 112 *P. cinereus* at 22 sites, 73 *P. cylindraceus* at 38 sites, and 14 salamanders that represent possible *P. hoffmani* x *P. virginia* hybrids at six sites. I found more than one species of *Plethodon* at 25 sites. Results suggest that *P. punctatus* is associated with rocky substrates, primarily among or near talus at high elevations. *Plethodon virginia* inhabits relatively dry ridges and slopes with deeper soil at all elevations. *Plethodon cylindraceus* is widespread throughout habitat types, while *P. cinereus* is scattered throughout the range in relatively mesic habitats. Similarly sized salamanders tended to not co-occur at the same sites, and had largely parapatric distributions. This apparent pattern of the exclusion of species from particular sites may be driven by competitive pressure coupled with differences in adaptation to climate.

Introduction

The genus *Plethodon* has undergone recent taxonomic expansion following the evaluation of genetic differences between populations of what are now considered separate cryptic species. Four species in the Valley and Ridge Physiographic Province in West Virginia have been described since 1972. In 1972, Highton described *P. hoffmani* and *P. punctatus* as new species based on morphological evidence. In 1989, Highton *et al.* recognized *P. cylindraceus* as a distinct species along with several others now recognized as separate species in the *P. glutinosus* complex based on an electrophoretic analysis of protein variation between populations. Highton conducted similar analyses on species in the *P. cinereus* group, which includes *P. hoffmani* and described *P. virginia* as a new species in 1999, which was previously considered to be *P. hoffmani*. After such revisions, *P. punctatus* has been considered a species of concern in West Virginia and Virginia due to its limited and disjunct range. *Plethodon virginia* has an overall range that is similar to that of *P. punctatus* (Highton 1999), but is not restricted to high elevations.

While several studies have been conducted to evaluate the life history and distribution of *P. punctatus* (Buhlmann et al. 1988; Pauley 1995, 1998; Tucker 1998; Flint 2004; Graham 2007), the distribution of *P. virginia* has received less attention because it was more recently described. The only study that has focused on *P. virginia* was by Fraser (1976a), who evaluated possible competition between *P. virginia* (then *P. hoffmani*) and juvenile *P. punctatus* on Shenandoah Mountain. Since that time, only Highton (1999) has discussed the natural history and distribution of this species. Because Fraser studied co-occurrence with *P. punctatus*, most information is restricted to the high elevation sites used in that study. Details on the distribution of *P. virginia* throughout its remaining geographical range, and occurrence with other species is lacking. Information on the distribution and natural history of *P. virginia* and its interactions with other species is important to provide for proper management of biodiversity and to develop baseline data to guide future research regarding this species.

While *P. virginia and P. punctatus* have limited ranges, and are endemic to a narrow region in the Valley and Ridge in West Virginia and Virginia, *P. cinereus* and *P. cylindraceus* are widespread and common throughout much larger ranges that span several states. While *P. cinereus* is common throughout most of its range, it is absent throughout much of the Valley and Ridge where *P. virginia* and *P. hoffmani* are more common (Highton 1972, 1999). Conversely, *P. cylindraceus* is common throughout the same area within the Valley and Ridge, although is less commonly found on high elevation ridges throughout the region. In this study, I conducted surveys in the Valley and Ridge of West Virginia in Pendleton, Hardy, and Hampshire counties to characterize the distribution of each species of *Plethodon* within this range and to evaluate possible factors that shape the distributions of these salamanders.

The objectives of this study were to 1) collect baseline data on the geographical distribution and natural history of *Plethodon* salamanders in the Valley and Ridge of West Virginia, 2) to use current and historical sites to evaluate potential patterns and trends in their distribution and interactions, and 3) to use these findings to develop testable hypotheses as to the causes of such trends and patterns for future research.

Methods

I surveyed for woodland salamanders in forested habitats within the Valley and Ridge Physiographic Province. To locate salamanders, I used daytime natural cover object searches in which I turned over rocks and logs that provide a moist daytime refuge for salamanders during periods of the year when woodland salamanders are active. In areas with especially rocky substrates, such as talus slopes, that create difficulty in detection of salamanders due to the abundance of cracks and crevices, I used nighttime visual encounter surveys (VES) in which the rocky substrates were carefully scanned with headlamps during or shortly following periods of rain. Woodland salamanders emerge from cover on wet nights to forage and mate, which warrants the use of VES on such nights. When walking over areas of deeper soil during VES, cover objects were turned.

I conducted surveys in Nathaniel Mountain Wildlife Management Area (WMA), Short Mountain WMA in Hampshire County, WV, Lost River State Park in Hardy County, George Washington National Forest in Hardy and Pendleton counties, WV, and in a very narrow portion of the Monongahela National Forest that lies east of the South Branch River in Pendleton County. I made an effort to sample sites at all elevations within each area, as well as all aspects and habitat types (riparian, slope, ridge) by using USGS topographic quadrangle maps to aid in locating areas to survey. Though I used a purposive sampling design, I made an effort to sample sites that were near roads and trails as well as sites that were considerable distances from roads and trails that included hikes to the tops of ridges that contained no roads or trails.

Upon detection, I hand-captured and identified salamanders and placed them in plastic zip-sealed bags to be measured on-site and I recorded the geographic locations of each site with a Garmin GPS60 receiver. I also identified and recorded the locations of all other amphibians and reptiles throughout surveys. For all woodland salamanders, I measured snout-vent length (SVL) from the anterior end of the snout to the posterior end of the cloaca, tail length from the posterior end of the cloaca to the end of the tail, and cranial width at the widest part of the jaw. I used a 10 g and a 30 g spring scale to measure mass. I measured relative humidity, air temperature, and soil temperature within the immediate vicinity of each captured salamander. I measured soil temperature with a digital pocket thermometer that was probed approximately 3 cm into the soil. To measure ambient temperature and relative humidity, I placed a digital thermohygrometer in the exact location where the salamander was captured (i.e. within depression under cover object, or on surface when salamanders were found without cover). If a salamander was found under a cover object, I recorded the cover object type (i.e. rock, log). Upon completion of measurements, salamanders were released at the point of capture.

Results

From March-November 2008, 321 woodland salamanders were recorded at 91 sites, including 74 *P. punctatus* at 23 sites, 48 *P. virginia* at 33 sites, 112 *P. cinereus* at 22 sites and 73 *P. cylindraceus* at 38 sites. Multiple species were found together at 25 sites. Because *P. virginia* has a zone of hybridization with a sibling species, *P. hoffmani*, at the southern extent of its range and the two species are indistinguishable in external characteristics (Highton 1999), those located within the vicinity of Reddish Knob in Pendleton County (sites: n = 6) are possible hybrids (n=14). There is also a zone of hybridization between these two species at the northern extent of *P. virginia*'s range, but the northern extent of the surveys were conducted south of hybrid populations recorded by Highton (1999). Environmental data were used in logistic regression models, which will be presented in the following study. Inventories of all amphibians and reptiles observed are presented in tables 5-10.

Plethodon punctatus

As in previous surveys, *P. punctatus* was limited to high elevations, and was located between 870 m on South Branch Mountain near Helmick Rock in Hardy County and 1267 m near Reddish Knob on Shenandoah Mountain in Pendleton County, which is within its known elevational range (Table 4; Figure 5). *Plethodon punctatus* was usually found either within or near talus slopes and rocky outcrops. Daytime cover surveys in rocky substrates with thin soil were relatively poor method to detect *P. punctatus* (Table 1). However, areas of deeper soil generally surrounded talus slopes and rocky substrates. When daytime cover object surveys were conducted in these areas, *P. punctatus* was detected more successfully. Nighttime VES were the most successful method in detecting *P. punctatus*; however, these searches were only reliable on wet nights, which limited the number of areas that could be surveyed per weather event with limited personnel.

George Washington National Forest

In the southern region of the George Washington National Forest, I found *P. punctatus* along the ridge of Shenandoah Mountain from 960 m to 1267 m in elevation. These surveys were conducted within the known range of *P. punctatus* (Figures 6, 7, 14, 16, 17).

In the northern region of the George Washington National Forest, 2 *P. punctatus* were captured just below the ridge of Great North Mountain in Hardy County (Figure 18). This location is of particular interest because, since the original description of the species by Highton in 1972, *P. punctatus* has not been reported from Great North

Mountain despite numerous surveys (Pauley 1995, Tucker 1998, Flint 2004, Graham 2007). The 2 salamanders were found on 11 October 2008 on a dry cool day (48% relative humidity, 18.3° C) under rocks in an area of relatively deep soil within the immediate vicinity of a talus slope (Figures 1, 23, 24). The exact same location had been surveyed the previous week on 4 October 2008, when one *P. cylindraceus* and seven *P. cinereus* were the only salamanders found. Other surveys along the ridge of Great North Mountain were unsuccessful in locating *P. punctatus*, but these were limited to daytime cover object searches in this region.

Other surveys

The only other area where *P. punctatus* was successfully detected was on Helmick Rock on South Branch Mountain in Hardy County (Figure 20). This is a site where this species has been found in past surveys. I surveyed this area with Casey Bartkus, who swabbed the ventral surface of each individual *P. punctatus* with a cotton-tipped epidural swab to survey for the presence of a chytrid fungus (*Batrachochytrium dendrobatidis*). We located 28 *P. punctatus* in a 7 hr-long VES along a talus slope. *Plethodon punctatus* were found active on the surface from 10:15 pm until between 3:00-3:30 am, when we stopped surveying due to exhaustion.

Nighttime VES were conducted for *P. punctatus* in two other areas, Lost River State Park, along Big Ridge (Figure 20), which consists of a ridge that is above 900 m in elevation for approximately 2 km and above 800 m for approximately 4 km, and along the ridges of Nathaniel Mountain and South Branch Mountain in Nathaniel Mountain WMA (Figure 19). The top of Big Ridge consists of narrow areas of rocky substrates and talus, and the slopes below consist of deep soil and areas of relatively rocky substrates. A VES was conducted on a rainy, foggy night on 13 July. Despite ideal conditions in what appeared to be suitable habitat, no *P. punctatus* were detected. The only salamander found was one *P. cylindraceus* near Miller Rock. The following day, several areas of deeper soil were searched in daytime cover surveys and again, only one *P. cylindraceus* was detected.

Visual encounter surveys conducted on a rainy night on 24 October in Nathaniel Mountain WMA were unsuccessful in detecting *P. punctatus* even though P. punctatus were historically found near the Nathanial Mountain lookout tower (Graham 2007). I conducted VES on 24 October in areas along the ridge of Nathaniel Mountain and South Branch Mountain where *P. punctatus* had not previously been detected. Surveys were conducted in and around areas of talus. The only salamanders found were one *P. virginia* and one *P. cylindraceus* on the ridge of South Branch Mountain at the southern extent of Nathaniel Mountain WMA. Daytime surveys were also conducted in areas where *P. punctatus* had previously been recorded in Nathaniel Mountain WMA near the Nathaniel Mountain lookout tower, but only *P. cylindraceus* were found in these areas.

Plethodon virginia

Plethodon virginia was found from 536-1106 m in elevation on ridges and slopes throughout its known range in West Virginia (Figures 8 & 9). The majority of *P. virginia* were detected during daytime cover object searches under rocks (Tables 1 & 2). Only two individuals were detected on the surface during VES, while three others were found during VES after turning natural cover objects in areas of deeper soil. From 12 June to 6 September 2008, only one *P. virginia* was detected at one site out of 24 sites surveyed within the range of *P. virginia*. During this period, salamanders that occur in the zone of hybridization in the vicinity of Reddish Knob near the Pendleton County, WV-Augusta County, VA border, which may represent *P. hoffmani* x *virginia* hybrids (Highton 1999) were located at six sites (Figure 15). Reddish Knob is the highest in elevation in the region, and is relatively cool and moist compared to other regions within the study area (Tucker 1998), and appears to contain the greatest abundance of woodland salamanders of all sites surveyed in 2008 (where *P. cinereus* and *P. punctatus* were also found). The majority of *P. virginia* detected were found during spring and fall surveys. Gravid females were found on 14 May, 25 October, and 7 November. Because females likely oviposit and guard eggs in the summer when they are rarely active on the surface (Fraser 1976a), finding gravid females in autumn suggests that female *P. virginia* likely have a biennial reproductive cycle as in *P. hoffmani* (Angle 1969).

George Washington National Forest

Historic sites for *P. virginia* within the George Washington National Forest are generally located along the higher elevations of Shenandoah Mountain, presumably because surveys for *P. punctatus* have been conducted in those areas. Several ridges and knobs run parallel to the ridge of Shenandoah Mountain approximately 2.5 km to the west, where there was little to no historical data on the presence of woodland salamanders. These ridges, including Heavener Mountain, Brushy Knob, Dunkle Knob, Fisher Knob and Ant Knob, which reach up to 760-920 m in elevation, seem to be considerably drier and hotter than the ridges of Shenandoah Mountain to the east. *Plethodon virginia* was the only small *Plethodon* found along these slopes and ridges, and was the only salamander found at the top of one of the ridges (Heavener Mountain). The only other woodland salamander found on these ridges and slopes was *P. cylindraceus* (Figures 16 & 17).

In spring 2008, several of the *P. virginia* detected within this area had blotches of reddish pigment along their dorsum. The dorsum in general had an indistinct brownish stripe that extended from directly behind the head to the area immediately posterior to the hind limbs (Figure 26). In the fall, however, individuals in this area lacked red blotching, and the brownish dorsal coloration diffused into the darker lateral color, which was nearly black, resulting into a less distinct stripe (Figure 2). It is unclear whether this is a natural variation between individuals or if the dorsal pattern of individuals may alter slightly across seasons. On 28 March 2008, an individual that was found at the base of Heavener Mountain and was presumably a young-of-the-year (SVL=20.2, Tail length=15.6), had a distinct narrow red stripe extending from directly behind the head to the area immediately posterior to the hind limbs (Figure 27). Highton (1999) states that *P. virginia* embryos sometimes have red stripes. It is likely that this individual was a *P. virginia*. The closest *P. cinereus* found was approximately 2 km away on the ridge of Shenandoah Mountain at a historic site. It seems likely that *P. virginia* in this area possess a gene or genes that result in a phenotypic red dorsal coloration that may fade with growth.

Nathaniel Mountain WMA

Six *P. virginia* were found in four sites in Nathaniel Mountain WMA in spring and fall surveys in the southern portion of the area on South Branch Mountain (Figure 19). Five of the individuals were found along the ridge of South Branch Mountain, while one was found in a ravine in a shallow valley between South Branch and Nathaniel Mountains. *Plethodon virginia* was sympatric with *P. cylindraceus* at two sites in this area. In the northern part of Nathaniel Mountain WMA *P. virginia* was not found while *P. cinereus* was found at two sites. It is possible that the two species are divided in the area, and presumably, there may be an area where they contact each other in-between. The two closest sites between the two species were approximately 1 km apart (Figure 19).

Lost River State Park

Four *P. virginia* were found at one site in Lost River State Park on 11 October 2008 (Figure 21). This site was located on East Ridge, which is in the southern part of Lost River State Park, and is divided from Big Ridge to the north by Howard's Lick Run, a second order stream. I did not detect *P. virginia* along Big Ridge and its associated slopes. *Plethodon cinereus* were found at the base of East Ridge within approximately 50 m of Howard's Lick Run. Within this area, the ridge-top site of *P. virginia* appeared to be a hotter and drier site than the sites where *P. cinereus* was found. *Plethodon cylindraceus* was found sympatrically with *P. cinereus* and *P. virginia* in sites associated with East Ridge. On 10 June, under a rock approximately 50 m from Howard's Lick Run where a female P. cinereus was found guarding eggs, a second salamander was found that might have been a *P. virginia* or a lead-back *P. cinereus*. The dorsum was dark with abundant brassy flecking, and the ventral surface was mostly dark with some white mottling. While the ventral surface was characteristic of *P. virginia*, the dorsal pattern did not have the appearance of an indistinct brownish dorsal stripe as did the individuals found on the ridge-top of East Ridge. The tail length was shorter than the SVL (SVL=42.4 mm, Tail length=41.1 mm), which is more characteristic of *P. cinereus*, but it could have been regenerated. *Plethodon virginia* was found only about 500 m from the nearest *P. cinereus*; more surveys will be needed to determine if this is an area where the distributions of *P. virginia* and *P. cinereus* may converge.

Monongahela National Forest

There is a narrow region in the Monongahela National Forest that is located east of the South Branch Potomac River in Pendleton and Grant counties. Five juvenile *P. virginia* (SVL ranged from 26.1-32.3 mm) were found at 3 sites on Cave Mountain in this area in northwestern Pendleton County (Figure 22). Cave Mountain is located immediately to the east of the South Branch Potomac River. No adult *P. virginia* were found in this area, but juveniles were characteristic *P. virginia*. At two of these sites, *P. virginia* were found sympatric with *P. cylindraceus*. The two juveniles captured on 12 June averaged 27.6 mm, while the individuals captured on 6 September averaged 32.0 mm, an increase of 4.4 mm over almost 3 months. These salamanders are presumably members of the same cohort.

Plethodon cinereus

Plethodon cinereus were found from 609-1310 m in elevation (Table 4; Figure 5). In the summer months, *P. cinereus* was only found in elevations above 890 m. *Plethodon cinereus* was typically found in higher elevations, and was only found below 750 m in 2 sites, and below 1000 m at only 7 sites out of 22 total sites where *P. cinereus* was detected (Figures 10 & 11). The two sites where *P. cinereus* were detected below 750 m were both near (within < 50 m) second-order streams and were sympatric with *P. cylindraceus*. Daytime cover object searches were the most successful means of detecting *P. cinereus*, and rocks were the most used cover objects (Tables 1 & 2).

George Washington National Forest

Within the southern part of the George Washington National Forest in West Virginia, *P. cinereus* was only found within the vicinity of Reddish Knob. Historically, *P. cinereus* has also been found in areas along the Shenandoah ridgeline farther north, but was not found north of a site between Bother Knob and Flagpole Knob in Rockingham County, VA. *Plethodon cinereus* was sympatric with *P. hoffmani* x *virginia* in 6 sites within this area (Figure 15).

Plethodon cinereus was the only small *Plethodon* found in the northern part of GWNF along the ridgeline of Great North Mountain. Of the 24 *P. cinereus* found at four sites on Great North Mountain, 11 (46%) were unstriped morphs. *Plethodon cinereus* was found sympatrically with *P. punctatus* and *P. cylindraceus* at one site on Great North Mountain (Figure 18).

Nathaniel Mountain WMA

Two *P. cinereus* were located at separate sites in Nathaniel Mountain WMA (Figure 19). One site was less than 50 m from a first-order stream that empties into Mill Run, a second-order stream, where *P. cinereus* was sympatric with *P. cylindraceus*. The other site was located in a ravine at the base of the northern most extent of South Branch Mountain. This salamander was about 1 km from the nearest *P. virginia* site to the southwest.

Lost River State Park

Plethodon cinereus was found at three sites at the base of East Ridge near Howard's Lick Run (Figure 21). *Plethodon cylindraceus* was sympatric with *P. cinereus* at two of these sites. As mentioned above, these sites are approximately 500 m from the nearest *P. virginia* site, which is located along the ridgeline of East Ridge. On 10 June, a female *P. cinereus* was found guarding a clutch of seven eggs under a rock (Figure 28). The eggs were hanging from what appeared to be a root in an opening in the soil. The eggs were whitish, and embryos did not appear to be far along in development, as the eggs appeared to only contain a whitish fluid. The female was coiled around the eggs. Interestingly, there was another salamander found under the same rock, which had the appearance of a *P. virginia*, but may have been a lead-back phase *P. cinereus* as described above. This salamander was not identified to species because it had characteristics that were intermediate to *P. virginia* and *P. cinereus*. Beacause P. virginia occur within 500 m of this sight on East Ridge. This could be due to natural variation, or potentially hybridization between *P. virginia* and *P. cinereus*. Further surveys need to be conducted to determine if *P. virginia* occurs at this site.

The remaining *P. cinereus* was found at a site about 5 km northwest of Lost River State Park at Helmick rock. Only one *P. cinereus* was found at this site during a VES in which one *P. cylindraceus* and 28 *P. punctatus* were also found.

Plethodon cylindraceus

Plethodon cylindraceus appears to be the most widespread woodland salamander in the area (Figures 12 & 13), although it was not found as commonly at higher elevations as in lower elevations. *Plethodon cylindraceus* was found from March through November between 540 and 890 m in elevation and was the only *Plethodon* found below 870 m between 13 July and 6 September. Historically, *P. cylindraceus* has been found at high elevations along the Shenandoah Mountain ridgeline, though infrequently (Tucker 1998), but was not found there during 2008 surveys. The highest elevation sites where *P. cylindraceus* was found during 2008 surveys were along the ridges of Great North Mountain in Hardy County and South Branch Mountain in Hampshire County. Daytime cover searches were the most successful in detecting *P. cylindraceus*, and rocks were the most used cover objects, as with the other woodland salamanders.

George Washington National Forest

In the southern part of George Washington National Forest in West Virginia, *P. cylindraceus* was never found above 800 m, while *P. punctatus* was the only large *Plethodon* found at high elevations. In the vicinity of Reddish Knob, only one *P.*

cylindraceus was found at one site on 27 March at 794 m elevation (Figure 14). *Plethodon cylindraceus* was commonly found at the bases of Shenandoah Mountain and the smaller ridges and knobs that run parallel to the west. In this area, *P. cylindraceus* was frequently found with *P. virginia* (Figures 16 & 17).

In the northern part of George Washington National Forest, along the ridge of Great North Mountain, *P. cylindraceus* was found at its highest elevation from 2008 surveys at 890 m (also found at this elevation on South Branch Mt. in Hampshire County) on 4 October (Figure 18). This same site area was surveyed one week later when *P. punctatus* was found; *P. cinereus* was also found at this site during both surveys.

Nathaniel Mountain WMA

Plethodon cylindraceus was found at six sites in Nathaniel Mountain WMA in Hampshire County (Figure 19). Within this area, *P. cylindraceus* was found along the ridge of South Branch Mountain, near two first-order streams that lead into Mill Run and within 10 m of Mill Run, a second-order stream. The individual found close to Mill Run was in a rock crevice in a rock outcrop on a steep slope with numerous rocky outcrops. *Plethodon cylindraceus* was sympatric with *P. virginia* at two sites and *P. cinereus* at one site in Nathaniel Mountain WMA. Three individuals were found at a site just below the ridge of South Branch Mountain in the vicinity of the Nathaniel Mountain lookout tower where *P. punctatus* has been found historically.

Short Mountain WMA

Plethodon cylindraceus was found at one site in Short Mountain WMA and was the only *Plethodon* found in this area. It was found at 680 m on 17 May. Historically, *P. cinereus* has also been found in this area.

Lost River State Park

Plethodon cylindraceus was found at five sites in Lost River State Park, though the three "sites" that were in the vicinity of Howard's Lick Run are close enough to be considered one site (Figure 21). In the northernmost area of Lost River State Park, near Miller Rock, two *P. cylindraceus* were found at 850 m elevation on Big Ridge on 13 July (Figure 20). These were the only *Plethodon* found after multiple surveys on Big Ridge. Near Howard's Lick Run between Big Ridge and East Ridge, *P. cylindraceus* was found with *P. cinereus* at two sites. *Plethodon cylindraceus* was sympatric with *P. virginia* on the ridge of East Ridge. *Plethodon cylindraceus* was also found 5 km to the northwest of Lost River State Park near Helmick Rock on South Branch Mountain where it was found sympatric with *P. punctatus* and *P. cinereus*.

Monongahela National Forest

Surveys were conducted on Cave Mountain, which is in a narrow section of the Monongahela National Forest that lies east of the South Branch Potomac River. *Plethodon cylindraceus* was found at six sites on Cave Mountain, and was sympatric with *P. virginia* at two sites (Figure 22).

Discussion

Salamanders in the genus *Plethodon* in the Valley and Ridge tend to occur on wooded ridges, slopes, and valleys throughout the region, but each of the four species encountered during this study appeared to be distributed in a unique way with regards to landscape characteristics. The patterns of distribution of salamanders belonging to particular size-guilds as discussed by Grobman (1944), Highton (1972), and Adams (2007) holds true for the woodland salamanders of this region, where two similarly sized species were sympatric at only eight sites, six of which were within close proximity near Reddish Knob, and potentially represent large populations of *P. cinereus*, *P. hoffmani*, and *P. virginia* (or hybrids) (Table 3). Conversely, 29 sites contained two differently sized salamanders. In both Lost River State Park and Nathaniel Mountain WMA, *P. cinereus* and *P. virginia* were found to be separated by only a short distance, and both were found with *P. cylindraceus* at each region (Figure 19). Between the two small species, *P. virginia* appeared to inhabit the hotter, drier regions, while *P. cinereus* was found in cooler, moister regions. In Nathaniel Mountain WMA for instance, *P. cinereus* was only found in areas near streams or in cooler ravines while *P. virginia* was typically found closer to ridges, which tend to receive greater degrees of insolation, and in turn create hotter and drier meso- and microclimates. These findings support suggestions made by Highton (1972, 1999) regarding the distributions of these two species in relation to climatic factors. In the more southern portion of the range of *P. virginia*, both *P. cinereus* and *P. virginia* have been found near the summit of Shenandoah Mountain, but the two have rarely been found at the same site. Highton (1999) suggested that one species may be encroaching on the range of the other, and that the species that is found in isolated populations is likely being replaced by the other. Highton (1972) discussed a possible isolated population of *P. cinereus* near Moorefield, WV, as possible evidence that *P. virginia* (then *P. hoffmani*) may be encroaching on *P. cinereus*. While it is difficult to determine whether isolated populations of *P. cinereus* occur in the Valley and Ridge without more thorough surveys, it appears that, instead of occurring in isolated populations, *P. cinereus* may penetrate the northern regions of the range of *P. virginia* in relatively moist and cool ravines. One area where *P. cinereus* does not appear to penetrate into the *P. virginia* range is just west of the summit of Shenandoah Mountain in Pendleton and southwest Hardy counties where *P. virginia* has been found.

There appear to be three possible trends in the distributional patterns of these two species: 1) that *P. virginia*, with its larger body size and apparently smaller clutch size is better adapted to the hot, dry region of the valley and ridge (Highton 1999); in areas where its range overlaps with *P. cinereus*, *P. virginia* tends to occur on hotter, drier regions within those areas, and neither species is expanding their range, 2) *Plethodon cinereus* is currently expanding its range into the Valley and Ridge, and has done so more successfully in the cooler, moister areas, which causes regions of range overlap where *P. virginia* occurs in hotter drier areas, and 3) *Plethodon virginia* is expanding its range into the range of *P. cinereus* and has done so more successfully in hotter, drier regions where it is better adapted. If climate is the major factor in shaping the ranges of these salamanders, and trends towards a warmer and drier climate are occurring, it is possible that *P. virginia* may become better adapted to regions that were once wetter and cooler, and their range may be expanding. Conversely, research on the interspecific interactions of *P. cinereus* has shown it to be an aggressively superior territorial competitor, potentially excluding other salamanders from high quality habitat through aggressive interference (Griffis & Jaeger 2008; Jaeger et al. 2002). However, this has not always been the case, for instance, *P. hubrichti*, a small endemic *Plethodon* that has a limited range in the Blue Ridge Mountains in Virginia, is superior in aggressive interactions with *P. cinereus* (Arif et al. 2007). Future studies that investigate behavioral interactions between *P. virginia* and *P. cinereus,* as well as abiotic climatic conditions, could provide insight into the causes of their distribution patterns. There are several localities that were found in this study in which closely occurring populations of *P. virginia* and *P. cinereus* could be monitored to determine how biotic and abiotic conditions may differ.

Though *P. cylindraceus* and *P. punctatus* co-occur in some sites, their distributions are clearly divided by elevation (Table 4; Figure 5). The vertical pattern of distribution of these species has been documented in previous studies (Tucker 1998), and has been discussed with similar species pairs such as *P. cylindraceus* and *P. metcalfi* (Hairston 1949) and *P. jordani* and *P. teyahalee* (Nishikawa 1985) in North Carolina. To the west of the Valley and Ridge, in the Allegheny Mountains and Plateau, *P. wehrlei* and *P. glutinosus* are found at low and high elevations (Pauley 1980; Green & Pauley 1987) and occur in similar habitats (Highton 1972). Within its restricted high elevation distribution, *P. punctatus* tends to be associated with rocky substrates and especially talus slopes, where it can be locally abundant (Flint & Harris 2005). Tucker (1998) studied the distribution and habitat of *P. punctatus* and concluded that it either occurs in several relict populations restricted by climatic factors that influence microhabitat characteristics such as such as soil moisture, or from potential competitive interactions with *P. cylindraceus*. Graham (2007) suggested that *P. punctatus* possibly became isolated in cooler, wetter climates at the tops of mountains during past hot and dry climatic conditions such as the Pliocene Epoch (approximately 2-5 million years before present), and may have been restricted from following the returning cooler moister climates to lower elevations due to competitive pressure from *P. cylindraceus*, and instead adapted to colder high elevation conditions by using talus slopes where they could burrow deep into the ground.

Competitive pressure in the Valley and Ridge may have a greater effect than in the moister and cooler regions of the Allegheny Mountains and Plateau if decreased moisture reduces the density of resources such as food and adequate microhabitat, and may result in the separation of the two species in vertical distribution. In the Allegheny Mountains and Plateau, greater moisture and cooler temperatures may allow species such as *P. glutinosus* and *P. wehrlei* to coexist at similar sites. Studies on habitat and behavior of *P. wehrlei* and *P. glutinosus* could provide information on potential niche partitioning that allows resources such as food or space two be divided between these similar species. In the Valley and Ridge, the larger *P. cylindraceus* may be better adapted to hotter and drier conditions (as may be the case *for P. virginia* and *P. cinereus*) because of greater protection from desiccation, and may be a superior competitor, but interspecific behavioral studies have not yet been conducted between these species.

Conclusions

The patterns of distribution of woodland salamanders appear to be non-random in that similarly sized species tend to not co-occur, and that the larger species in each case (*P. cylindraceus* and *P. virginia*) appear to inhabit hotter and drier regions. *Plethodon* *virginia* is widespread throughout its range and occurs at all elevations along high and medium elevation ridges and slopes and ravines, though it was observed in relatively low numbers. Within the range of *P. virginia*, *P. cinereus* is restricted to higher elevations along Shenandoah mountain and in cool and moist ravines and slopes near streams in lower elevations. *Plethodon punctatus* is restricted to high elevation ridges in the area, primarily along the ridge of Shenandoah Mountain, and in several apparently disjunct populations on Jack Mountain, Great North Mountain, and South Branch Mountain. *Plethodon cylindraceus* is widespread throughout the Valley and Ridge, but is not as common on high elevation ridges where *P. punctatus* is typically found.

Table 1. Number and percentage of each *Plethodon* detected in daytime cover object surveys (DTCS) and visual encounter surveys (VES) from March-November, 2008 in the Valley and Ridge of West Virginia.

Species	**DTCS**	**VES**
Plethodon punctatus	32 (43%)	42 (57%)
Plethodon virginia	43 (90%)	5 (10%)
Plethodon cinereus	88 (79%)	24 (21%)
Plethodon cylindraceus	61 (84%)	12 (16%)

Table 2. Number and percentage of each *Plethodon* found under cover object types from March-November 2008 in the Valley and Ridge in West Virginia. Percentages only include salamanders found under cover, and do not include salamanders that were found active on the surface.

Species	**Rock**	**Log**	**Other***
P. punctatus	26 (81%)	4 (13%)	LL=1, B=1
P. virginia	39 (91%)	4 (9%)	NA
P. cinereus	62 (70%)	22 (25%)	B=3
P. cylindraceus	50 (82%)	10 (16%)	RC=1

* LL=leaf litter, B=bark, RC=rock crevice

Table 3. Number of sites in which species were found at the same site in all surveys from March-November, 2008 in the Valley and Ridge in West Virginia.

Species	***P. cylindraceus***	***P. virginia***	***P. cinereus***	***P. hoffmani x virginia***
P. punctatus	2	1	9	4
P. cylindraceus	.	9	6	0
P. virginia	.	.	0	0
P. cinereus	.	.	.	6

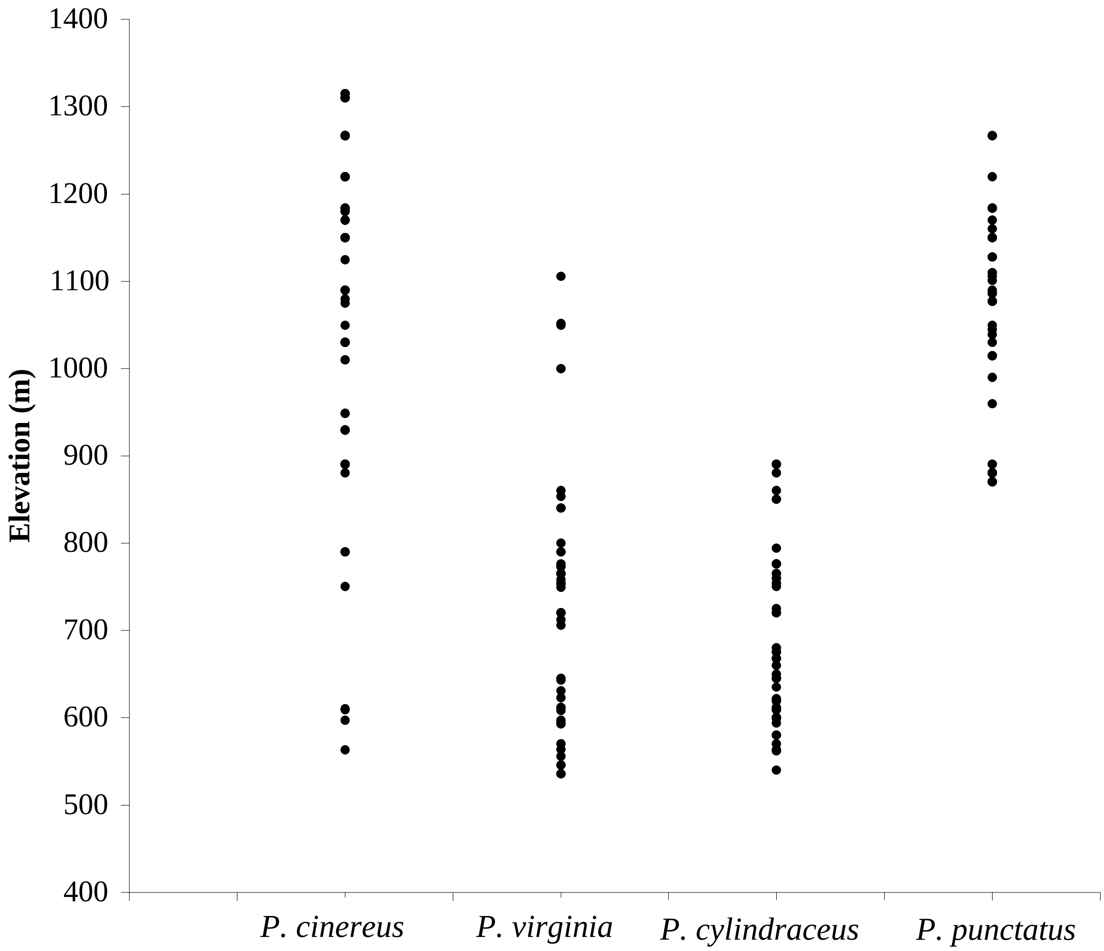


Figure 5. Elevational distribution of sites occupied by woodland salamanders in the Valley and Ridge in West Virginia, 2008.

Table 4. Number of *Plethodon* salamanders detected by elevational range from all surveys from March-November, 2008 in the Valley and Ridge in West Virginia.

Elevation (m)	***P. punctatus***	***P. cylindraceus***	***P. virginia***	***P. cinereus***
1100-1315	26	0	1	65
875-1099	36	6	4	27
700-874	12	21	25	16
< 700	0	46	18	4

Table 5. Inventory of amphibians and reptiles located in the George Washington National Forest in surveys from March-November, 2008 in Pendleton and Hardy counties in West Virginia.

Taxon	**n**	**County**	**Habitat and notes**
Caudata			
Eurycea bislineata	1	Pendleton	Hillside by stream
Notophthalmus v. viridescens	16	Pendleton, Hardy	Wooded hillsides and ridges (efts)
Plethodon cinereus	106	Pendleton, Hardy	High elevation ridges and slopes
Plethodon cylindraceus	28	Pendleton, Hardy	Wooded hills, ravines, and ridges
Plethodon punctatus	46	Pendleton, Hardy	High elevation ridges and slopes, rocky
Plethodon virginia	33	Pendleton	Wooded hillsides and ridges
*Plethodon hoffmani x virginia**	14	Pendleton	High elevation ridges and slopes
Pseudotriton ruber (adult)	1	Pendleton	Wooded hillside
Anura			
Rana clamitans	1	Pendleton	Near woodland pond (possibly ephemeral)
Rana palustris	1	Pendleton	Near woodland pond (possibly ephemeral)
Squamata			
Diadophis punctatus edwardsii	2	Pendleton, Hardy	Wooded hillside
Sceloporus undulatus	1	Pendleton	Hot, dry ridge-top

* Represents individuals from zone of hybridization (Highton 1999), genetic analysis is necessary to adequately identify individuals to species

Table 6. Inventory of amphibians and reptiles located in Lost River State Park in surveys from May-October, 2008 in Hardy County, West Virginia.

Taxon	n	Habitat and notes
Caudata		
Notophthalmus v. viridescens	2	Wooded hillsides and ridges (efts)
Plethodon cinereus	3	Wooded hillside near stream
Plethodon cylindraceus	12	Wooded hills, ravines, and ridges
Plethodon virginia	4	Wooded ridge

Table 7. Inventory of amphibians and reptiles located in the Nathaniel Mountain Wildlife Management Area in surveys from May-October, 2008 in Hampshire County, West Virginia.

Taxon	**n**	**Habitat and notes**
Caudata		
Notophthalmus v. viridescens	2*	Wooded hillsides and ridges (efts) *(also larvae in a breeding pool)
Plethodon cinereus	2	Wooded ravine, near stream
Plethodon cylindraceus	19	Wooded hills, ravines, and ridges
Plethodon virginia	6	Wooded hillsides ravines and ridges
Squamata		
Diadophis punctatus edwardsii	1	Syntopic w/ *P. cylindraceus* under rock on hillside

Table 8. Inventory of amphibians located in Short Mountain Wildlife Management Area in surveys in May 2008 in Hampshire County, West Virginia.

Taxon	**n**	**Habitat and notes**
Caudata		
Notophthalmus v. viridescens	Several	Adults in breeding pool
Plethodon cylindraceus	1	Flat wooded area
Anura		
Bufo americana	5	2 adults in amplexus, 3 adults in amplexus, in shallow pools with eggs
Hyla versicolor	2-3	Trees around shallow pools, captured 1
Pseudacris crucifer	Several	Shallow wetland/flooded field, 2 adults found in amplexus
Pseudacris feriarum	Several	Shallow wetland/flooded field, identified by call
Rana clamitans	Several	Wetland, identified by call

Table 9. Inventory of amphibians and reptiles located in the Monongahela National Forest in surveys from June-September, 2008 in Pendleton County, West Virginia.

Taxon	**n**	**Habitat and notes**
Caudata		
Notophthalmus v. viridescens	2	Wooded hillside (efts)
Plethodon cylindraceus	12	Wooded hillsides
Plethodon virginia	5	Wooded hillsides
Anura		
Bufo americana	1	Wooded hillside

Table 10. Inventory of amphibians and reptiles located in the Valley and Ridge in West Virginia in remaining sites in 2008.

Taxon	n	County/area	Habitat and notes
Caudata			
Ambystoma maculatum	1	Hampshire, Edward's Run WMA	Hillside by flooded field and ponds
Notophthalmus v. viridescens	2	Hardy, Helmick Rock; Hampshire, Edward's Run WMA	Wooded hillsides and ridges (efts)
Plethodon cinereus	1	Hardy, Helmick Rock	Talus slope
Plethodon cylindraceus	1	Hardy, Helmick Rock	Talus slope
Plethodon punctatus	28	Hardy, Helmick Rock	Talus slope
Anura			
Bufo americana	1	Hampshire, Edward's Run WMA	Wooded hillside
Bufo fowleri	1	Hardy, South Branch WMA	Sandy riverbank
Squamata			
Coluber c. constrictor	1	Pendleton	Roadkill
Elaphe obsoleta	2	Hardy, South Branch WMA	Hardy: roadkill SBWMA: juv. in weedy old field
Testudines			
Chrysemys picta	4	Hampshire, Edward's Run WMA	Basking on exposed log in pond

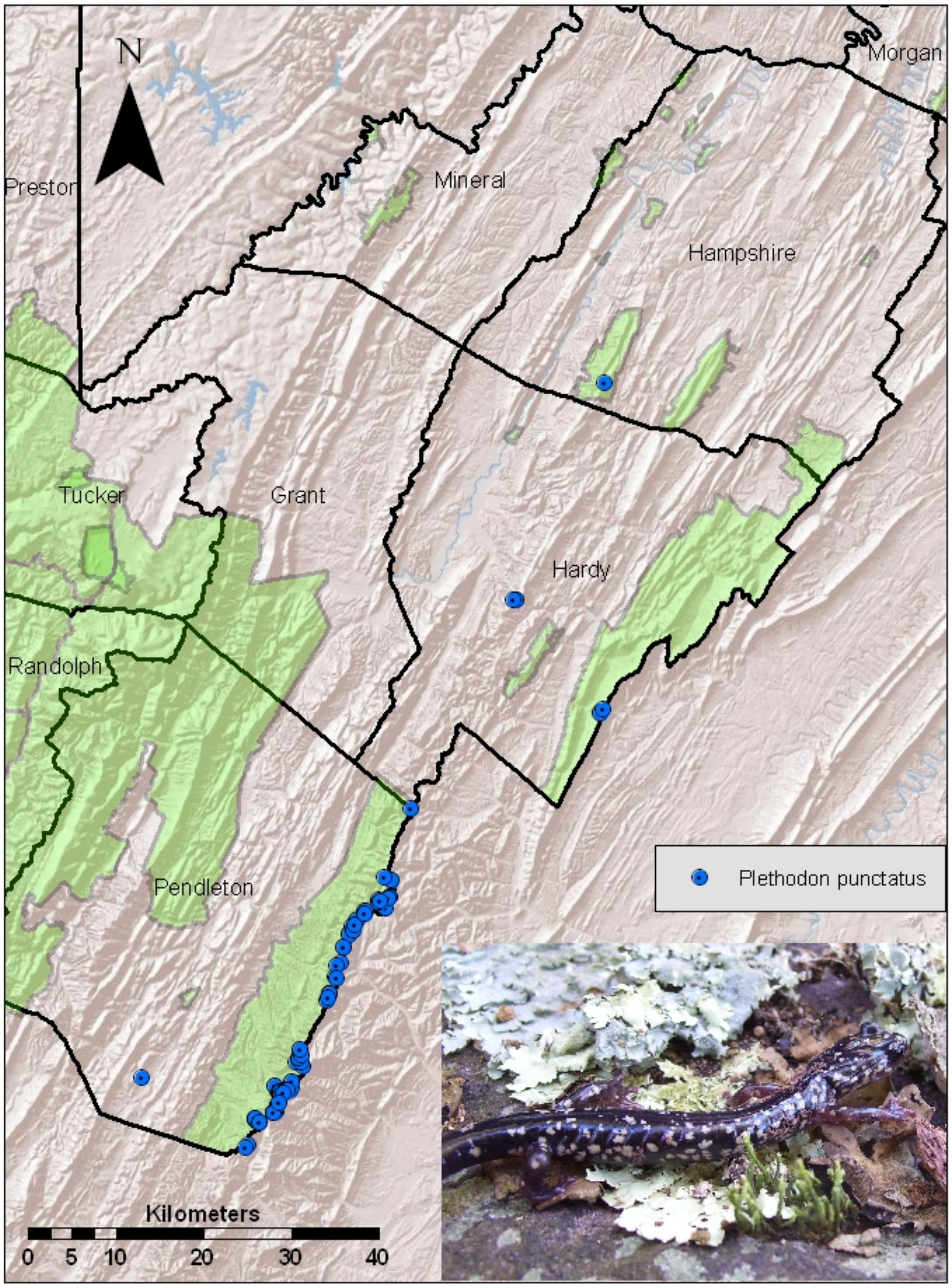


Figure 6. Current and historic site localities of *Plethodon punctatus* in West Virginia. Sites were compiled from the United States National Museum of Natural History records, past surveys by TK Pauley (1995, 1998), Marshall University graduate students (Tucker 1998, Graham 2007), and 2008 surveys conducted for this study.

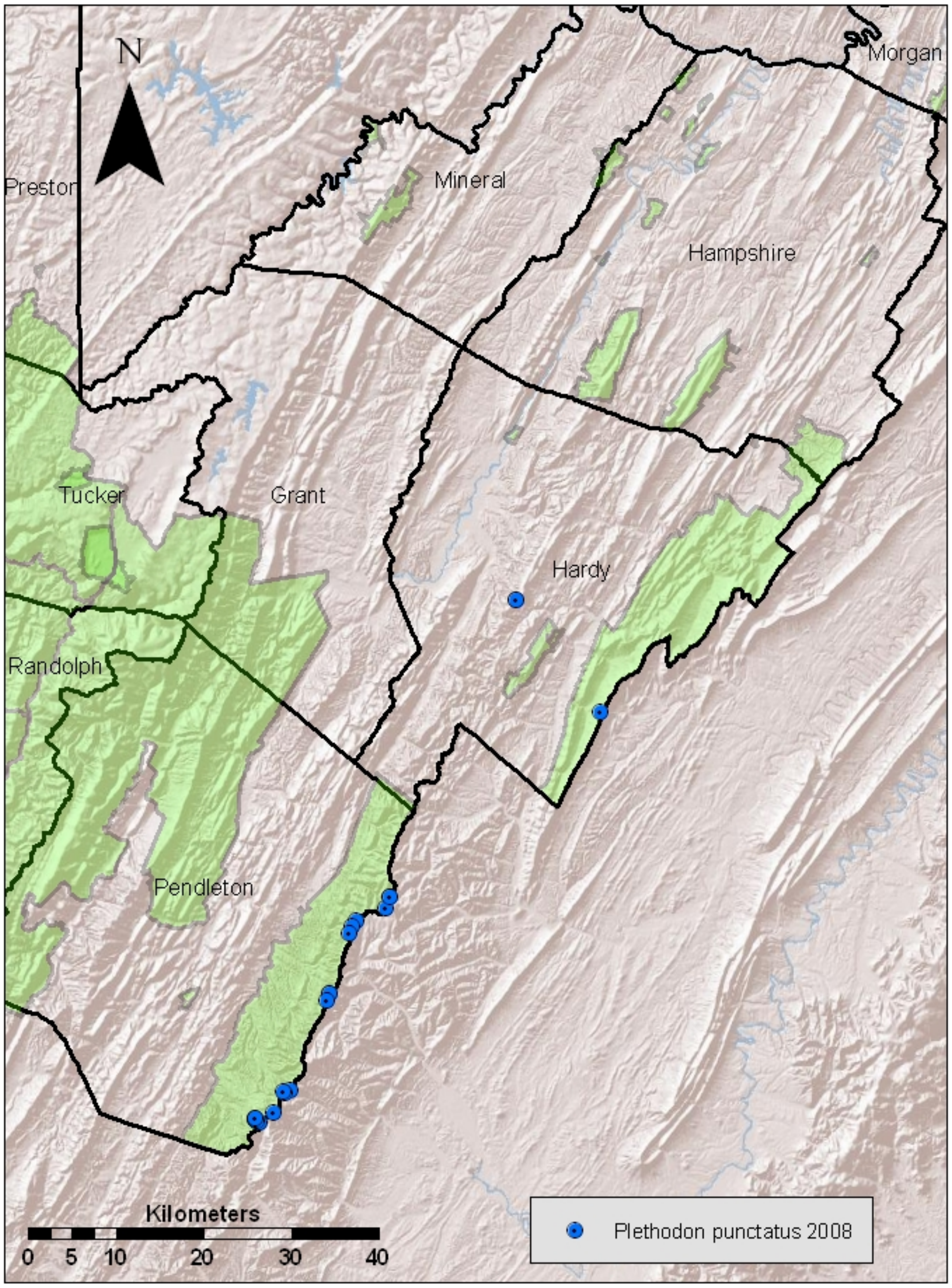


Figure 7. Site records for *Plethodon punctatus* in West Virginia from 2008 surveys.

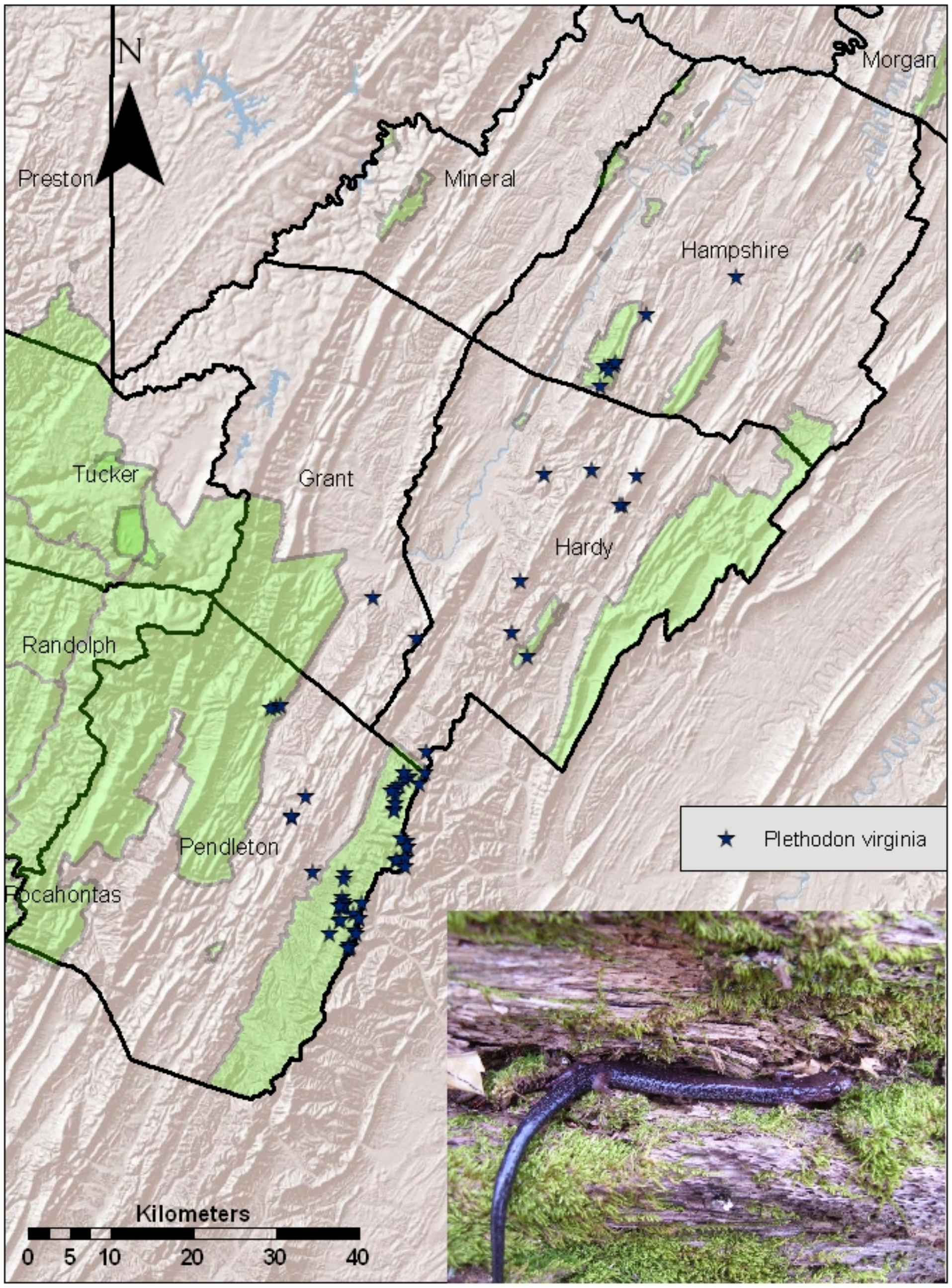


Figure 8. Current and historic site localities of *Plethodon virginia* in West Virginia. Sites were compiled from the United States National Museum of Natural History records, past surveys by TK Pauley (1995, 1998), Marshall University graduate students (Tucker 1998, Graham 2007), and 2008 surveys conducted for this study.

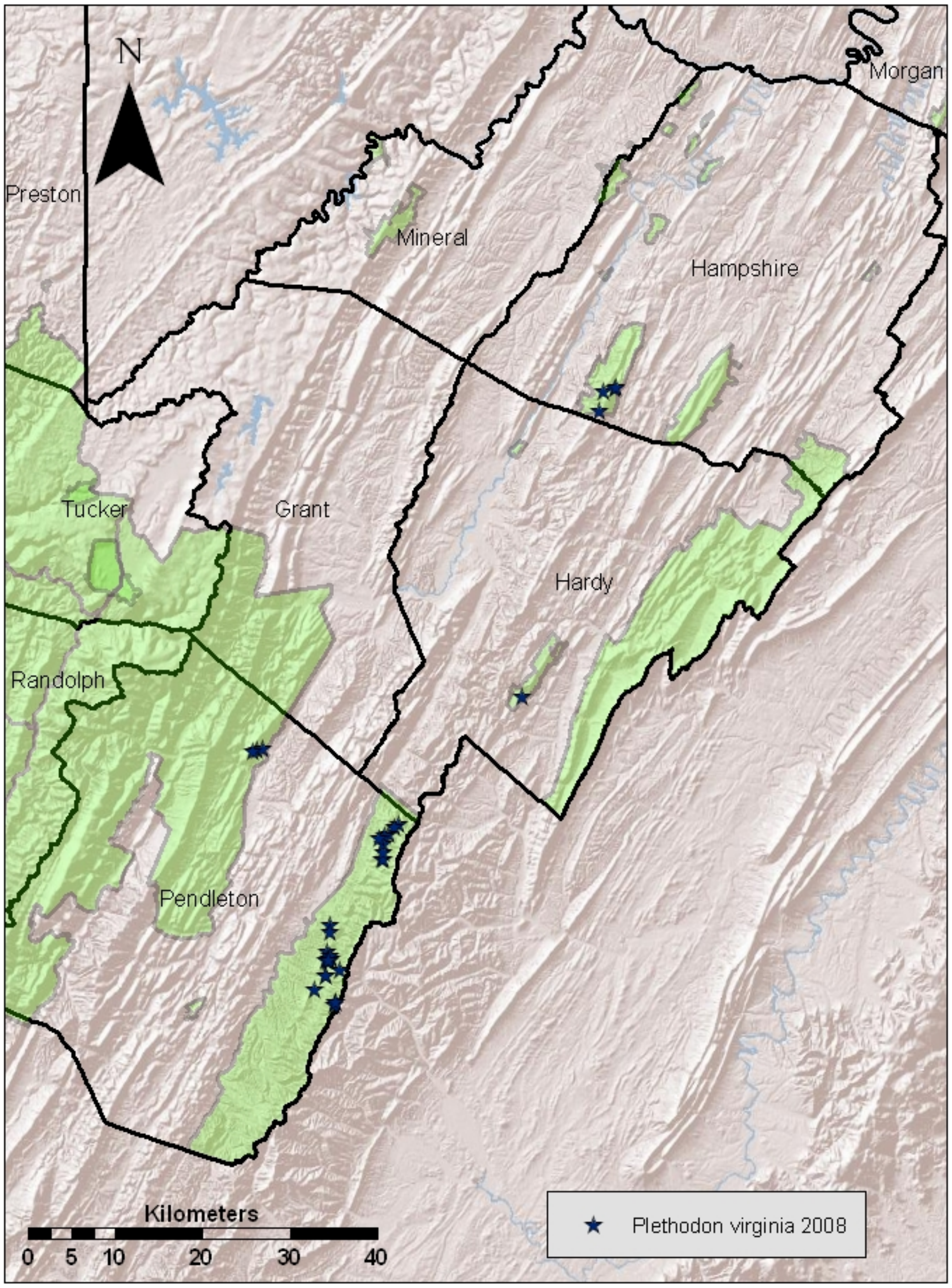


Figure 9. Site records for *Plethodon virginia* in West Virginia from 2008 surveys.

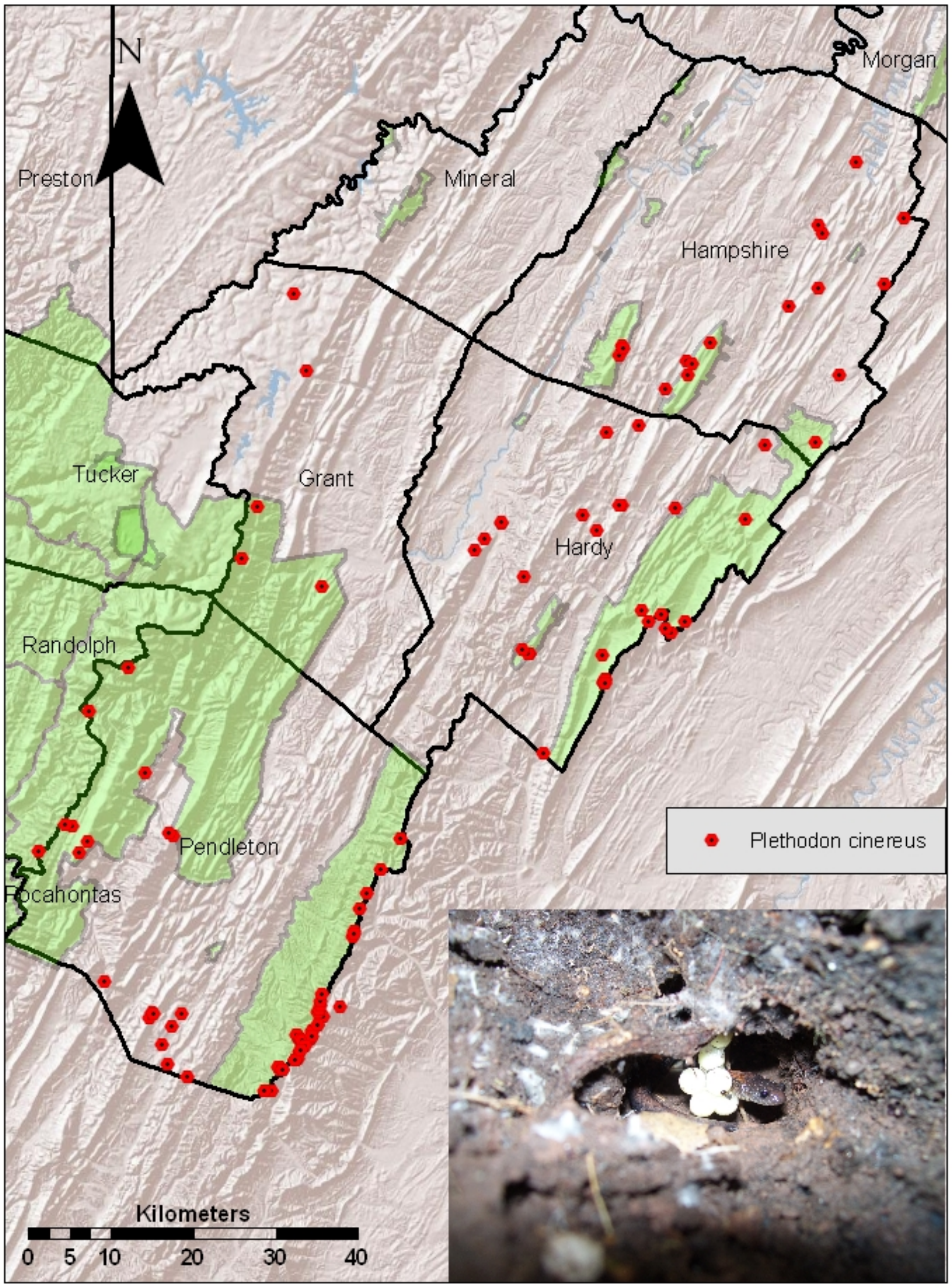


Figure 10. Current and historic site localities of *Plethodon cinereus* in Pendleton, Hardy, and Hampshire counties, West Virginia. Sites were compiled from the United States National Museum of Natural History records, past surveys by TK Pauley (1995, 1998), Marshall University graduate students (Tucker 1998, Graham 2007), and 2008 surveys conducted for this study.

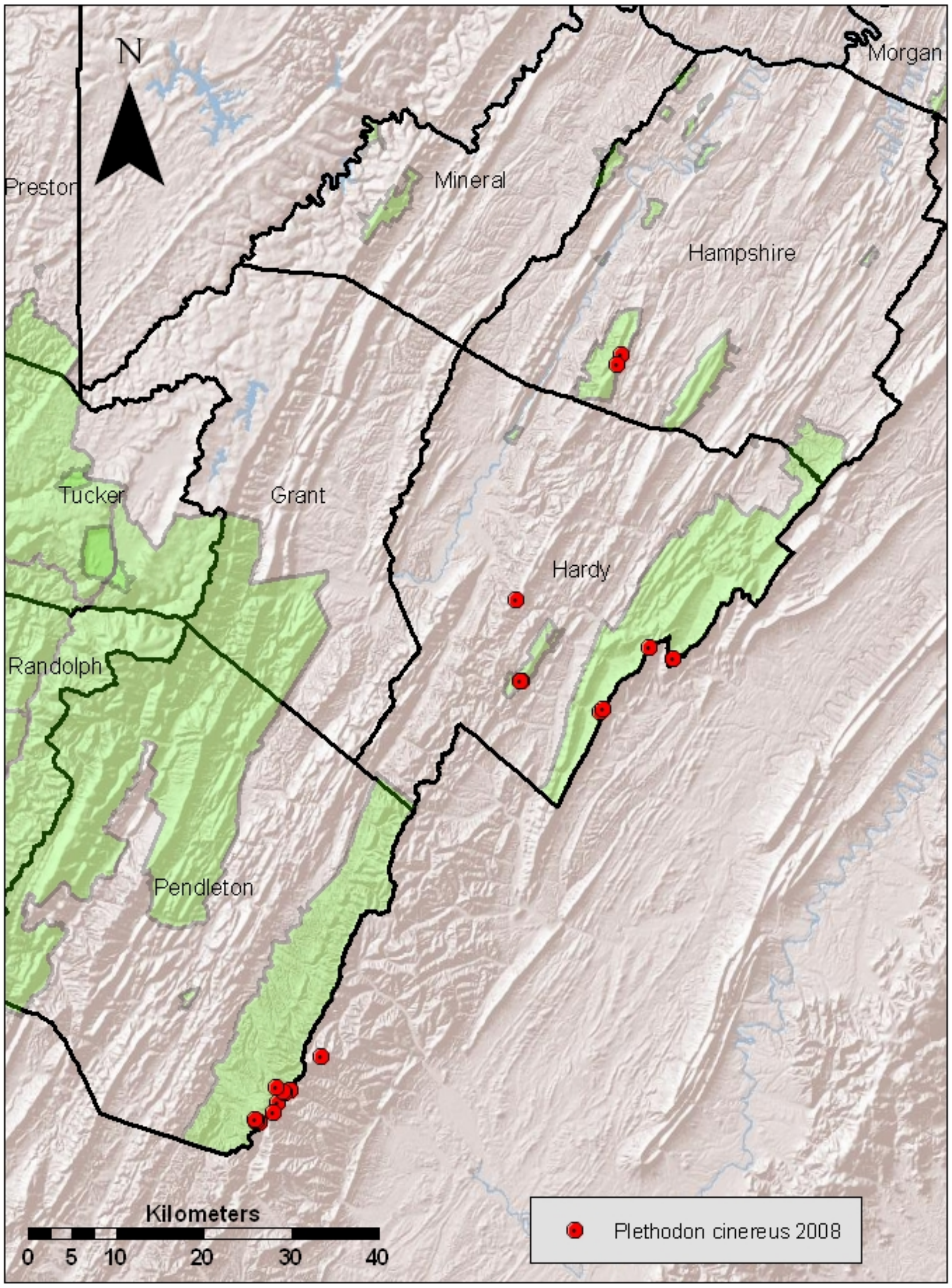


Figure 11. Site records for *Plethodon cinereus* in West Virginia from 2008 surveys.

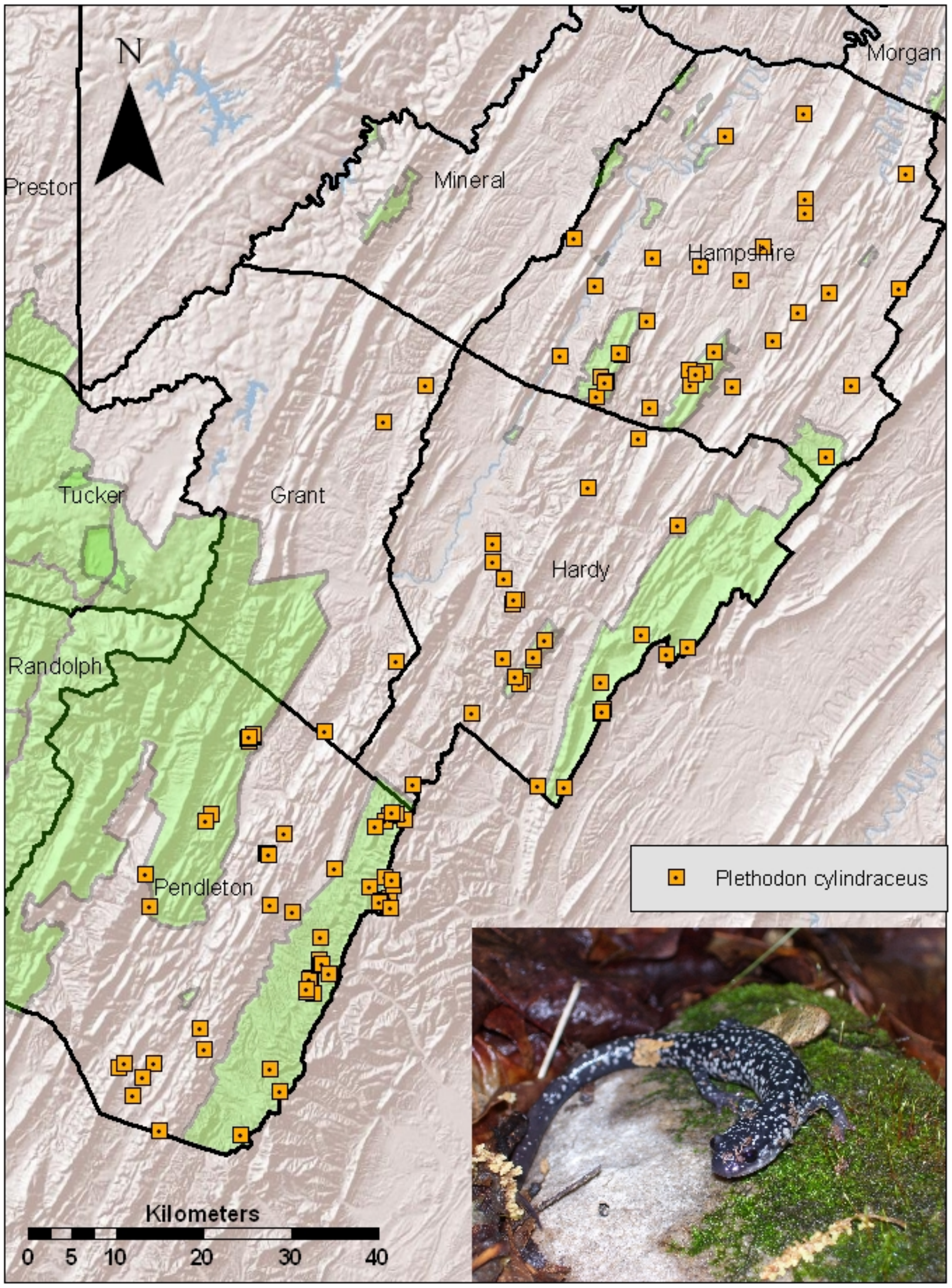


Figure 12. Current and historic site localities of *Plethodon cylindraceus* in West Virginia. Sites were compiled from the United States National Museum of Natural History records, past surveys by TK Pauley (1995, 1998), Marshall University graduate students (Tucker 1998, Graham 2007), and 2008 surveys conducted for this study.

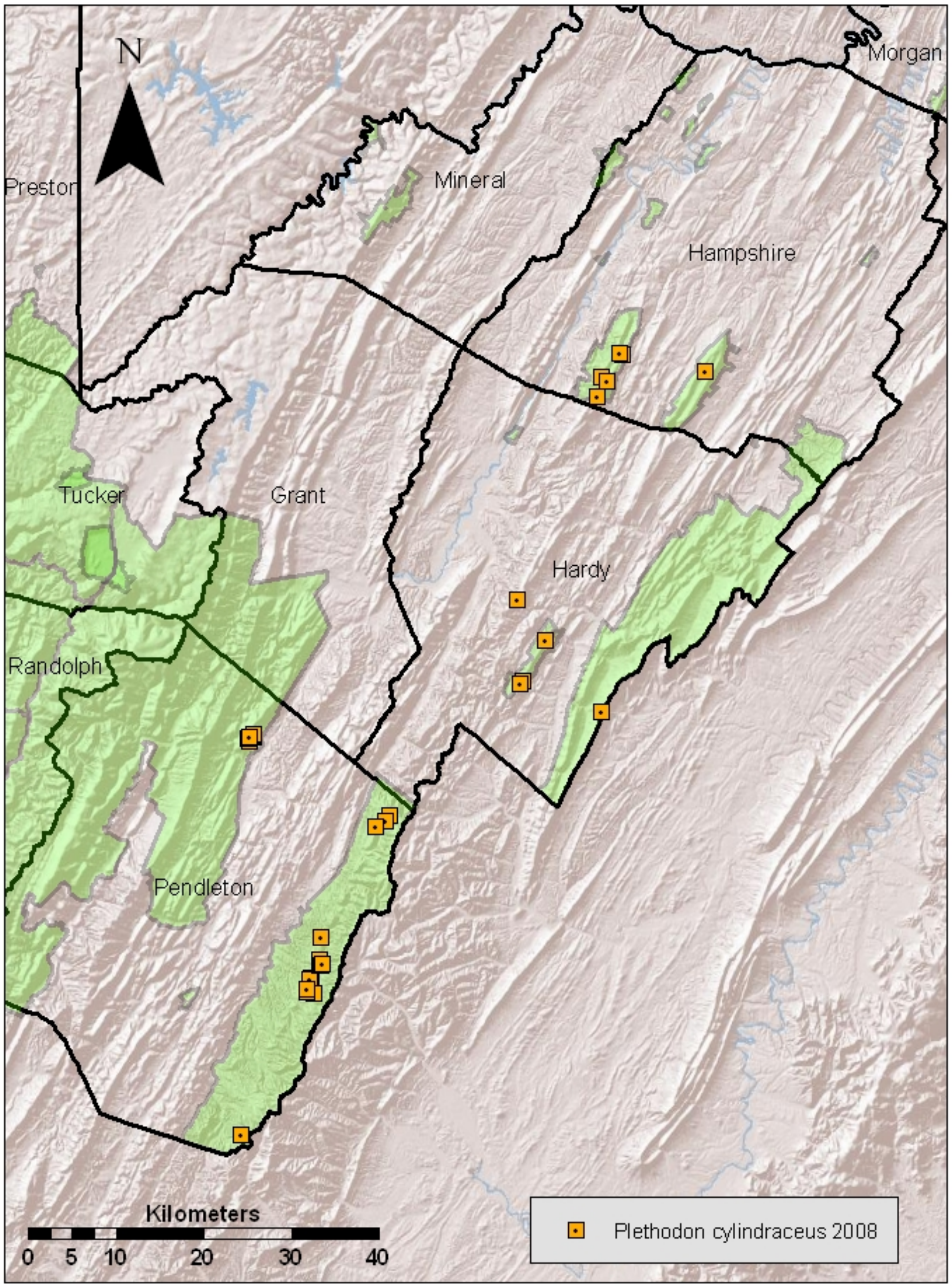


Figure 13. Site records for *Plethodon cylindraceus* in West Virginia from 2008 surveys.

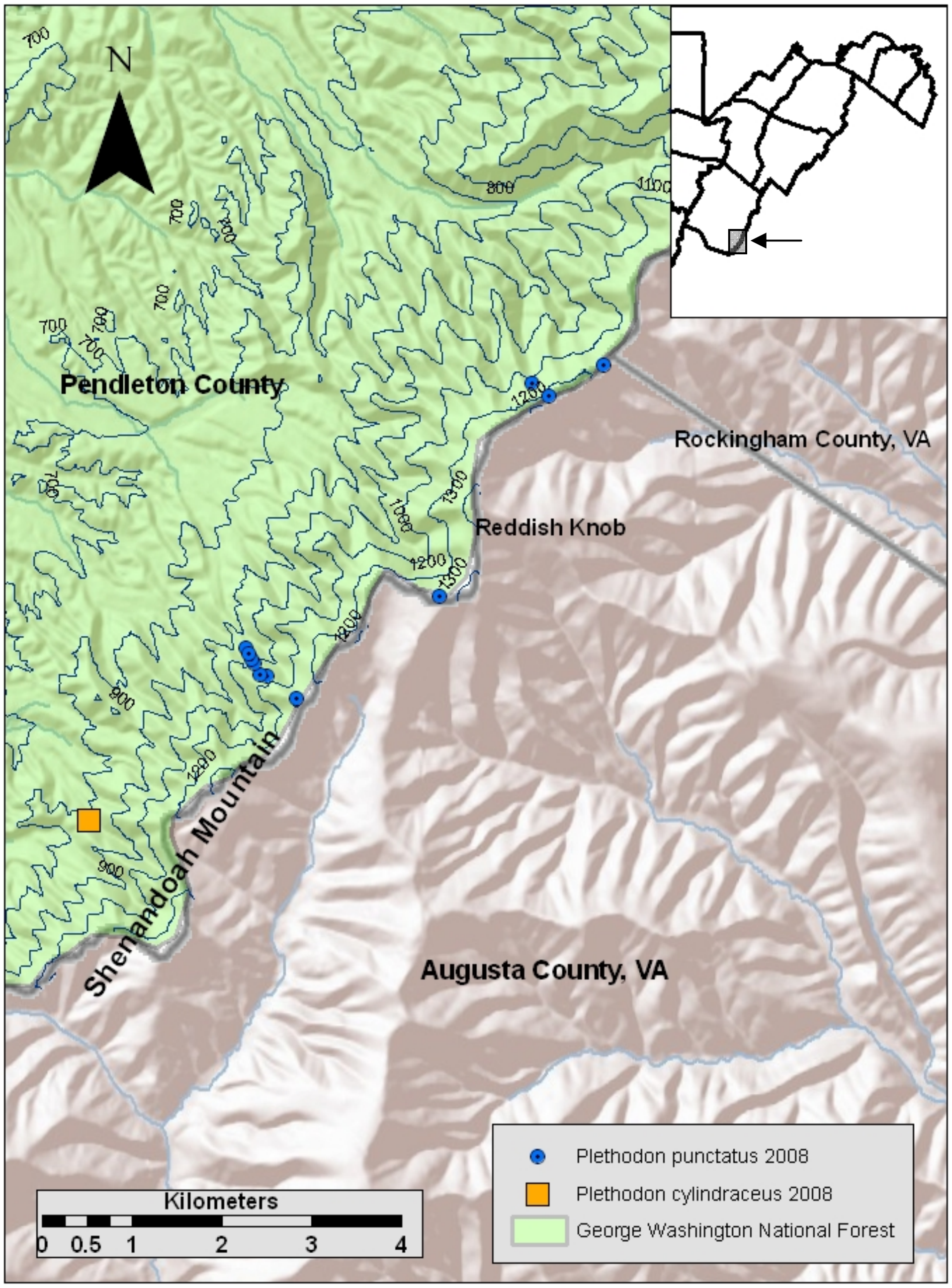


Figure 14. Large *Plethodon* occurrence sites from the vicinity of Reddish Knob on Shenandoah Mountain from 2008 surveys.

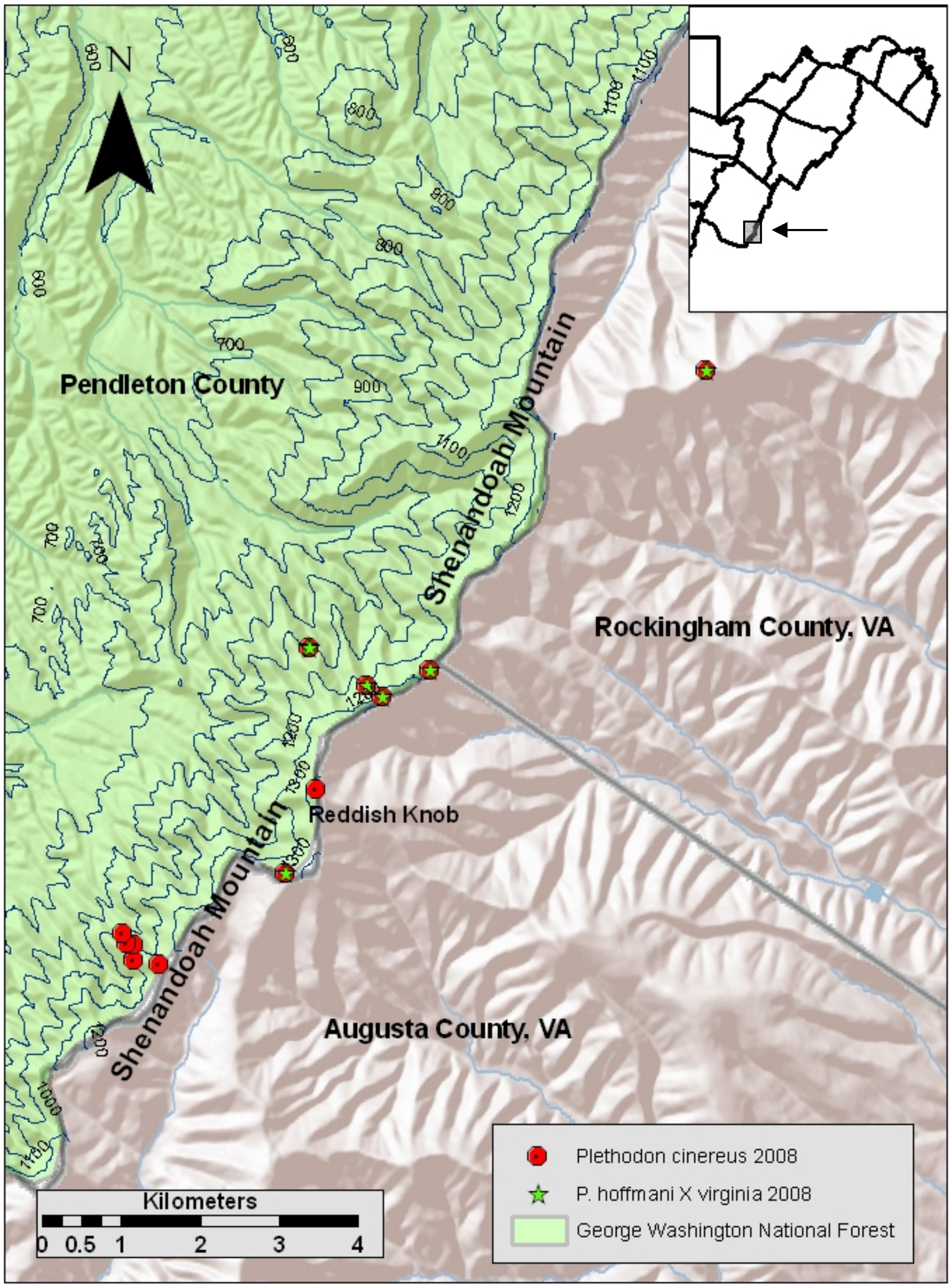


Figure 15. Small *Plethodon* occurrence sites in the vicinity of Reddish Knob on Shenandoah Mountain from 2008 surveys. *Plethodon hoffmani* x *virginia* localities represent possible hybrids based on the description of the distribution of *P. virginia* by Highton (1999).

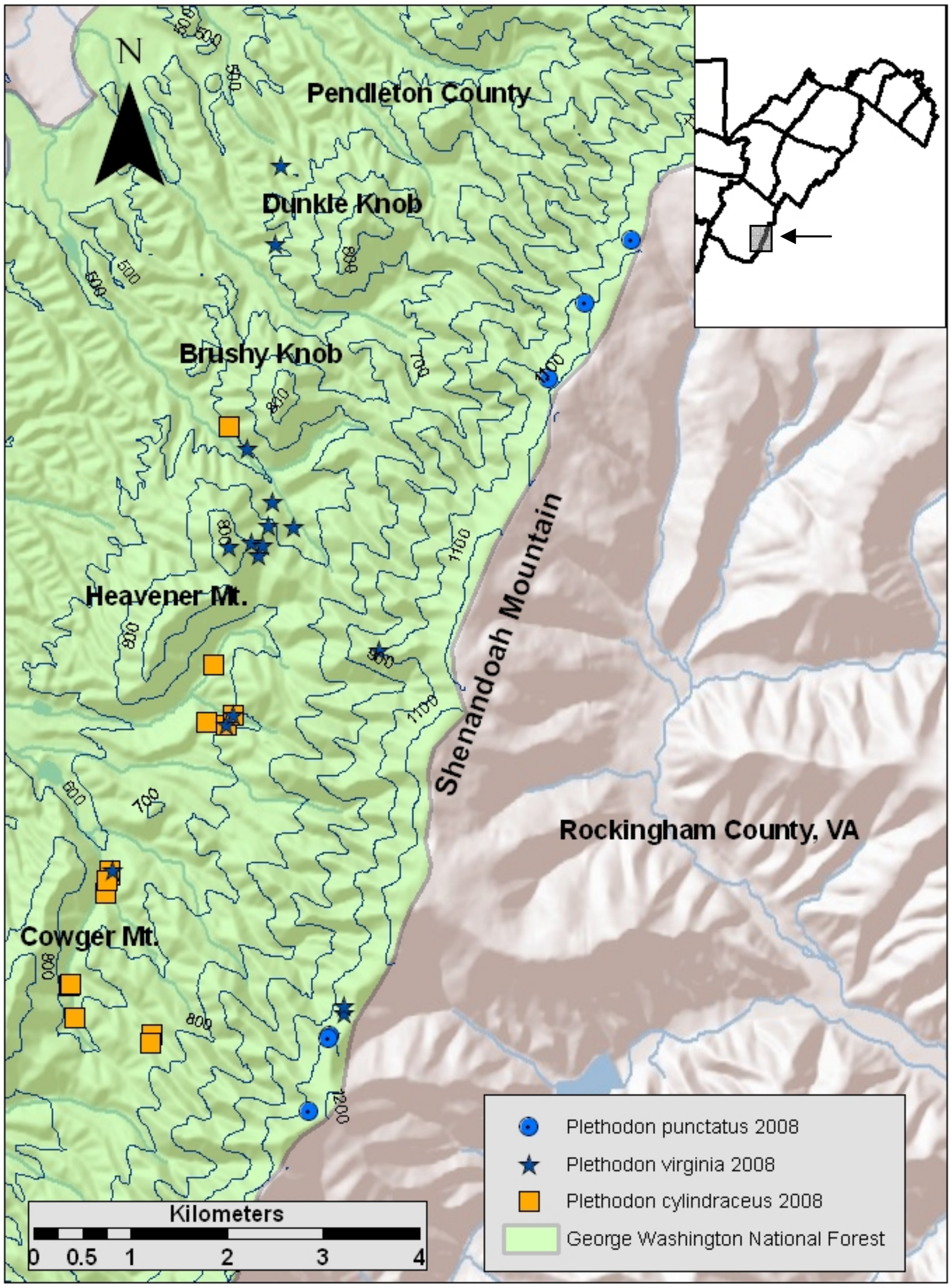


Figure 16. *Plethodon* occurrence sites east of Brandywine, WV on Shenandoah Mountain and ridges to the west from 2008 surveys

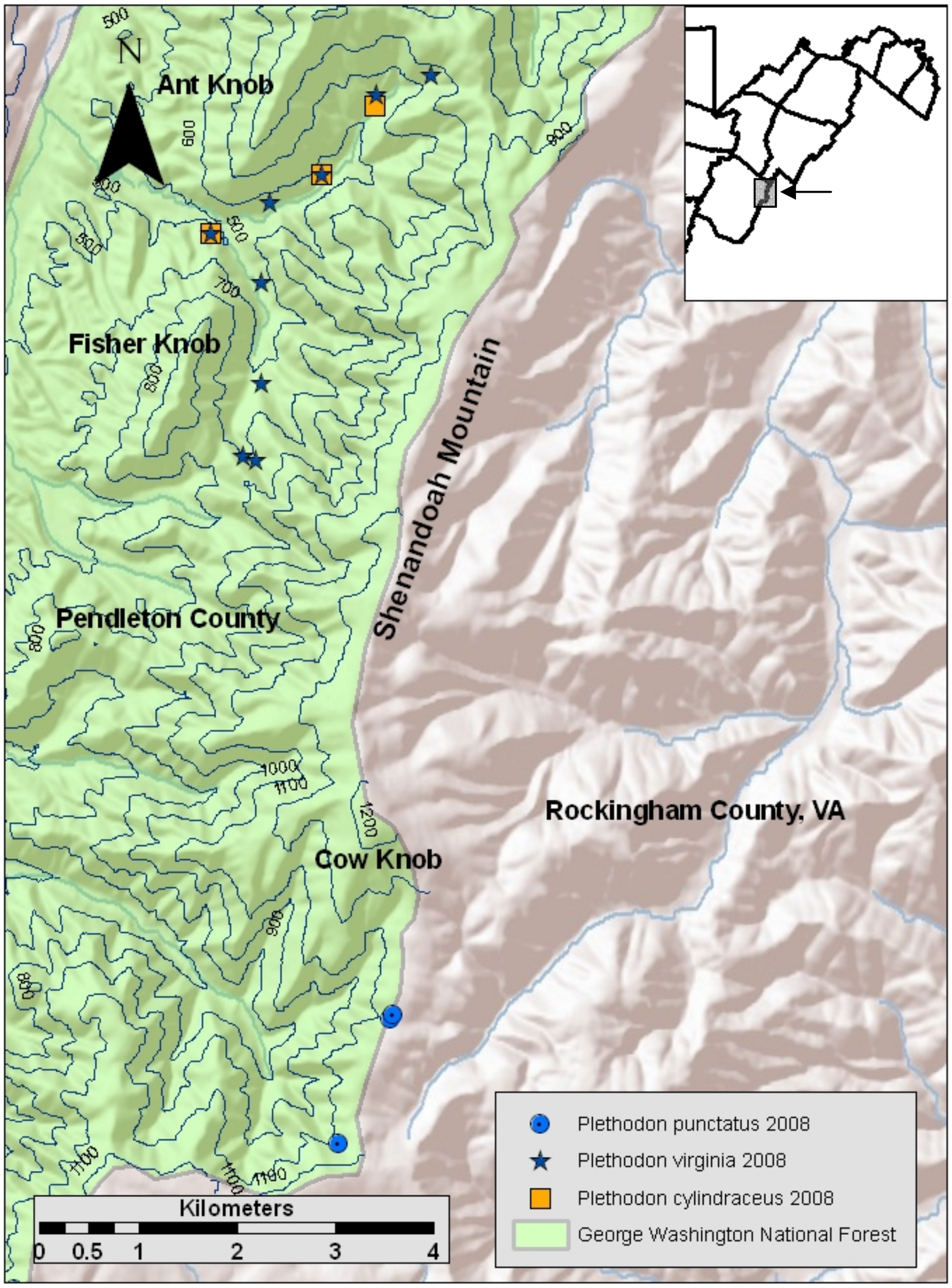


Figure 17. *Plethodon* occurrence sites in the vicinity of Cow Knob on Shenandoah Mountain and ridges to the west from 2008 surveys.

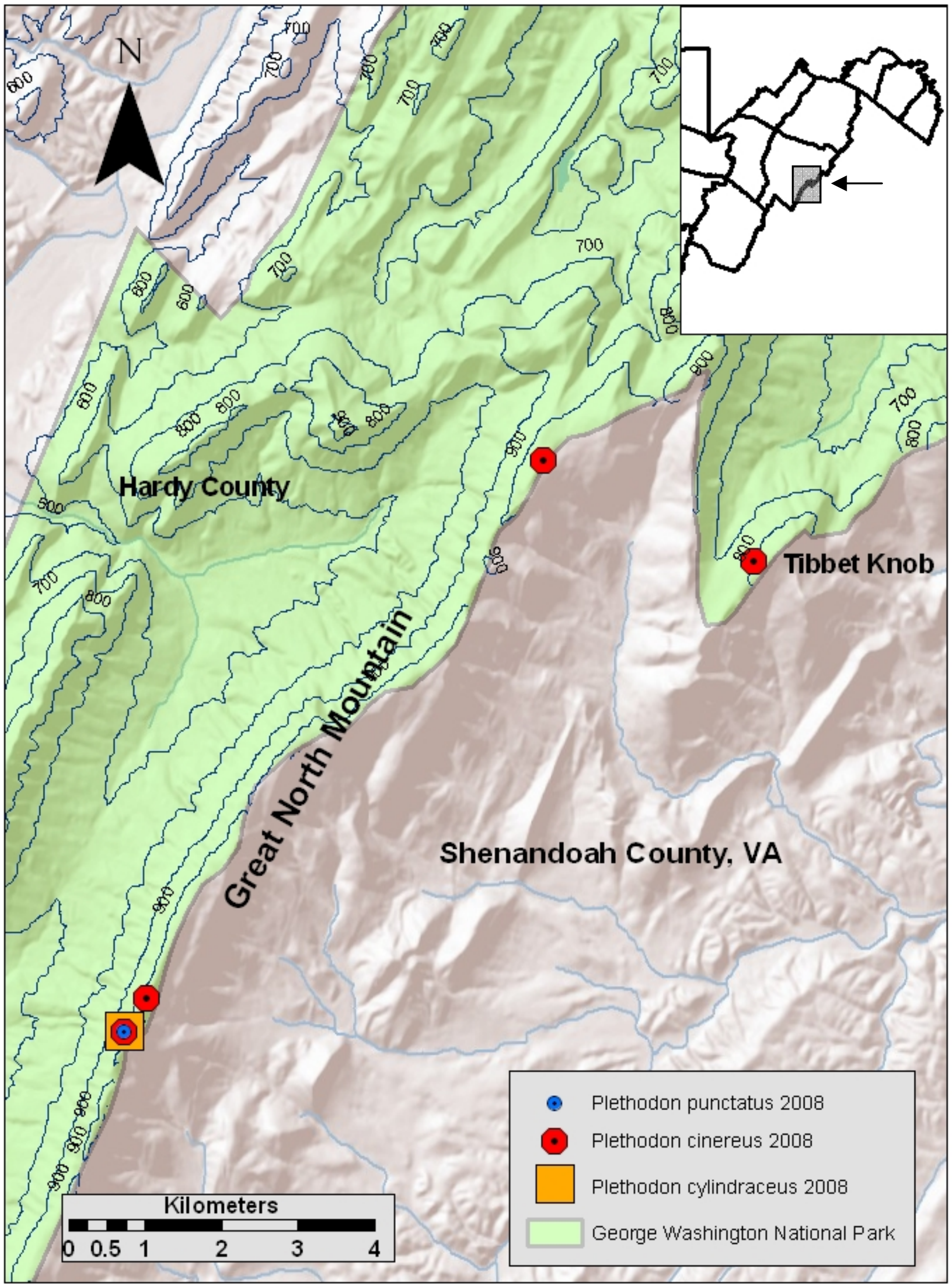


Figure 18. *Plethodon* occurrence sites on the ridge of Great North Mountain, East of Basore, WV from 2008 surveys

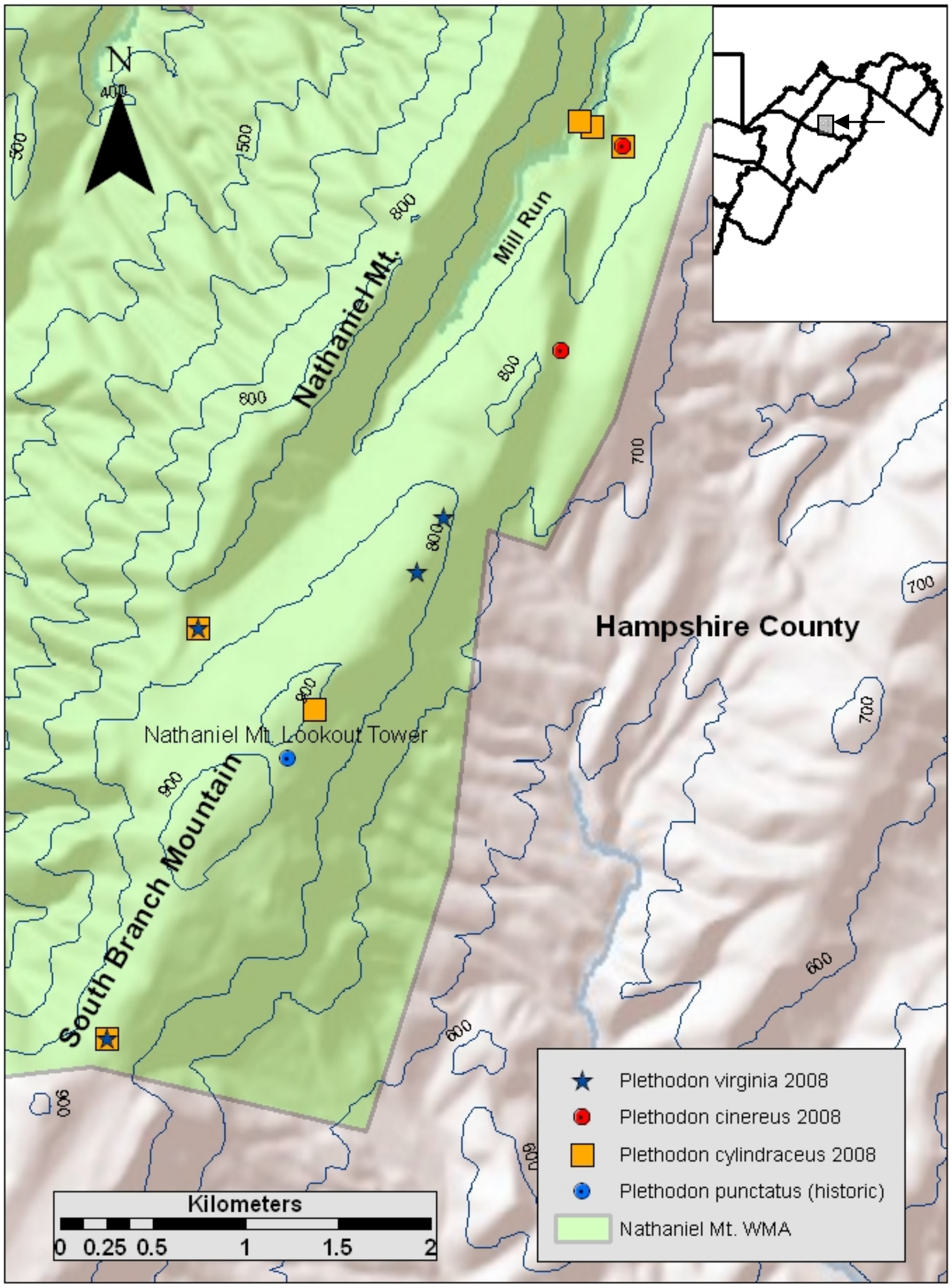


Figure 19. *Plethodon* occurrence sites from Nathaniel Mountain Wildlife Management area from 2008 surveys. The *P. punctatus* site shown is a historic site.

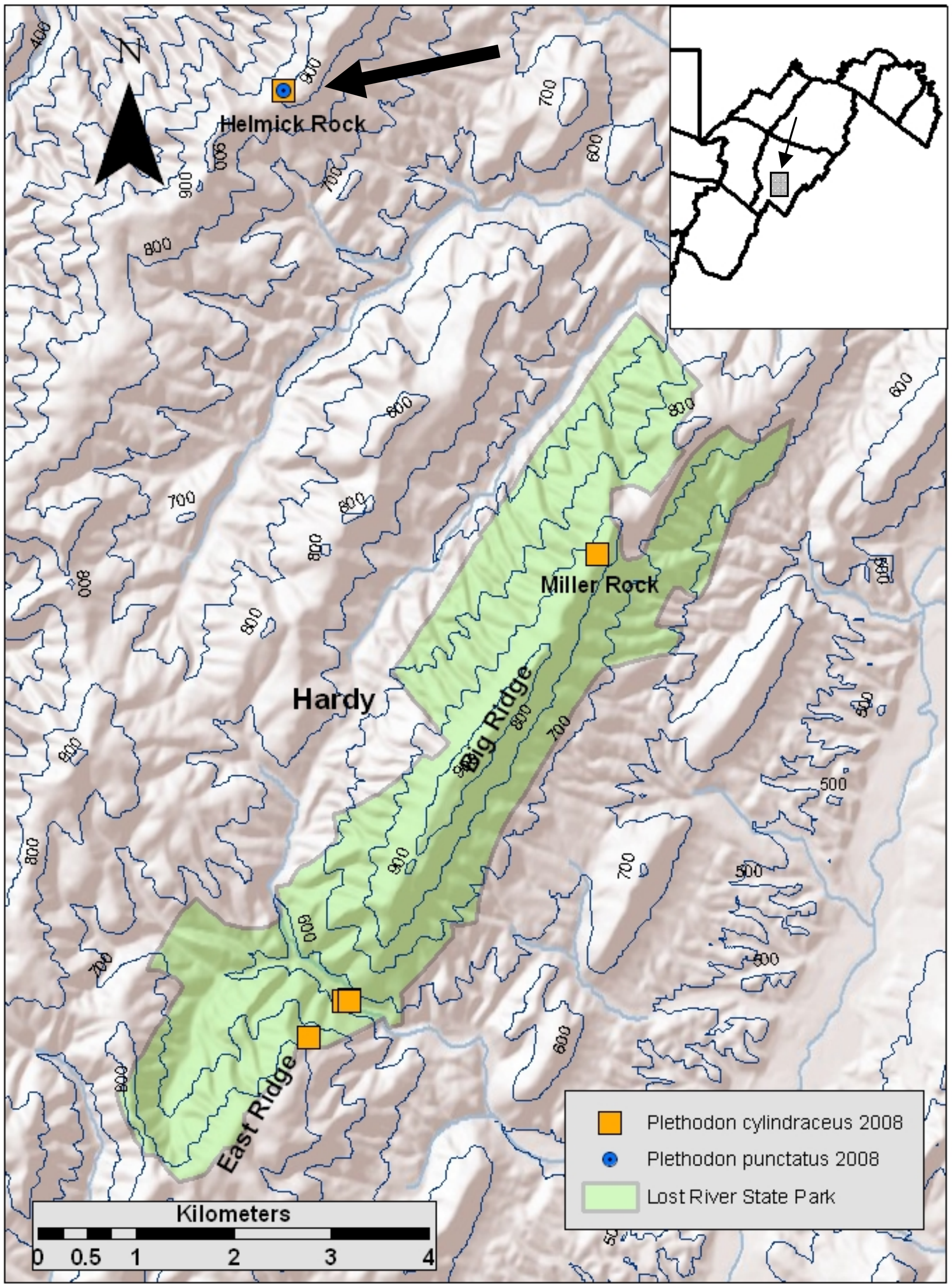


Figure 20. Large *Plethodon* occurrence sites from Lost River State Park and Helmick Rock to the northwest (where *P. cinereus* was also found) from 2008 surveys.

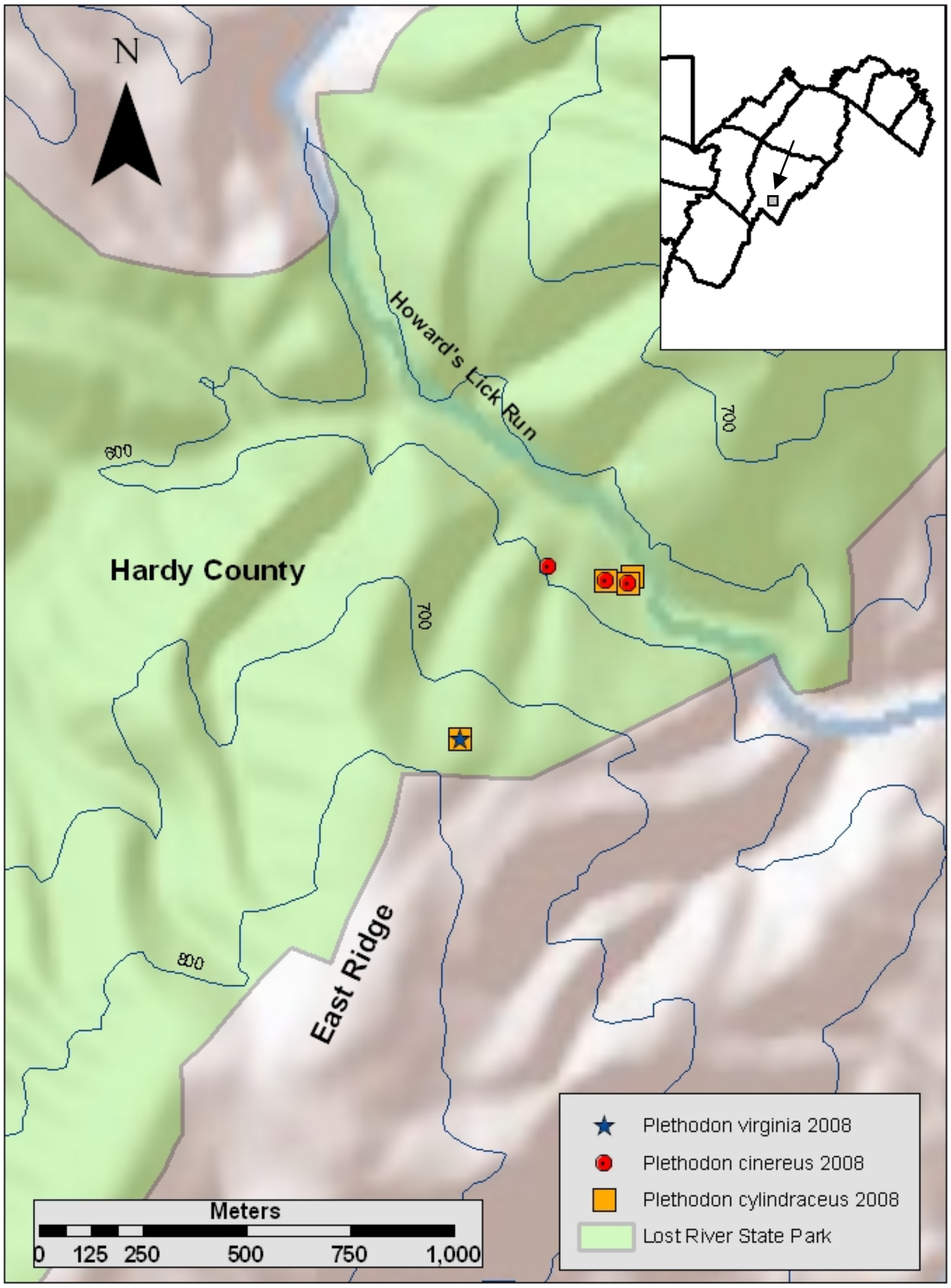


Figure 21. *Plethodon* occurrence sites in the vicinity of East Ridge in Lost River State Park from 2008 surveys.

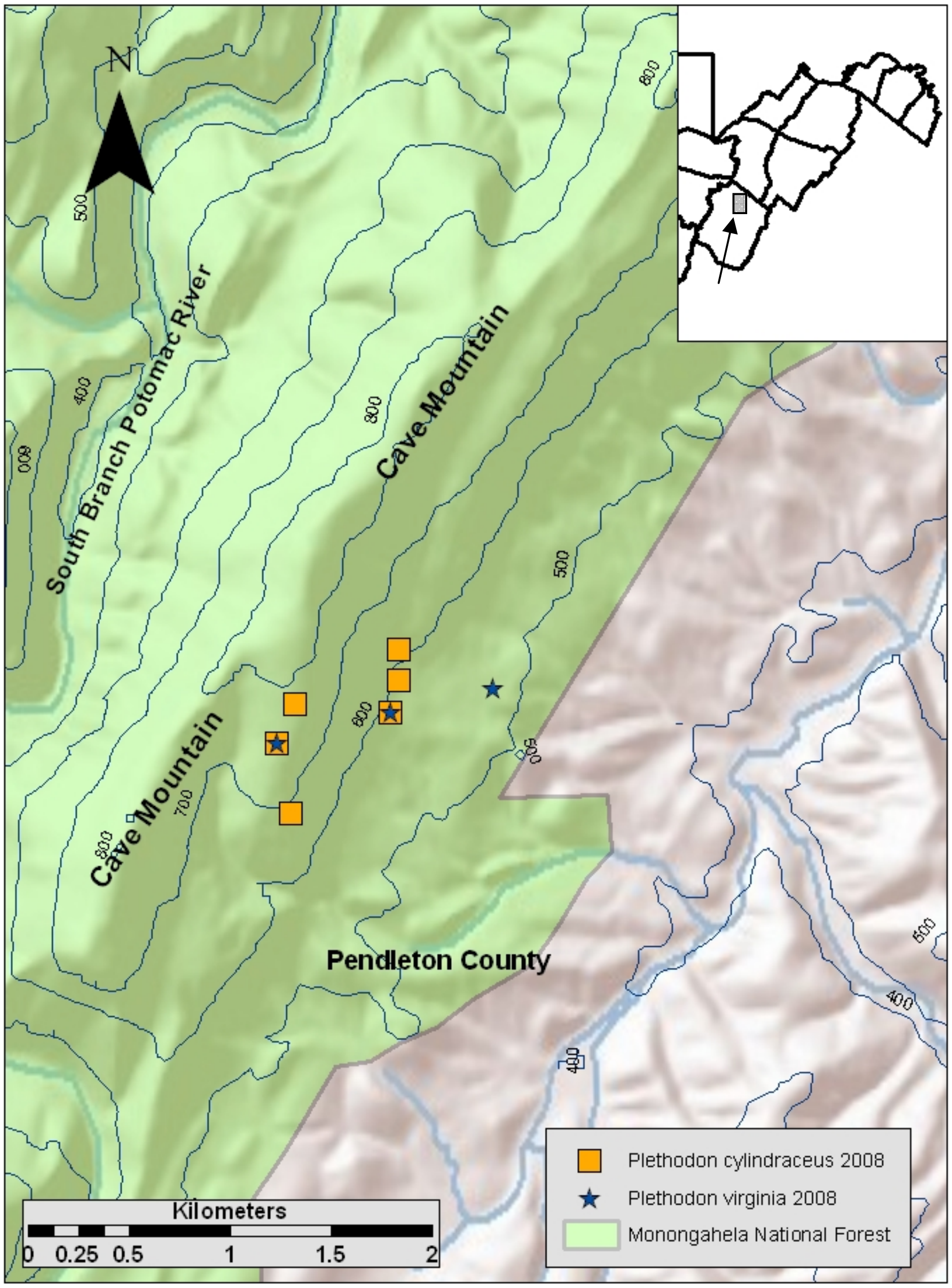


Figure 22. *Plethodon* occurrence sites from Monongahela National Forest on Cave Mountain from 2008 surveys.

Figure 23. *Plethodon punctatus* found on Great North Mountain, Hardy County, WV, November 2008.

Figure 24. Picture of site where *Plethodon punctatus* was found on Great North Mountain, Hardy County, WV, November 2008.

Figure 25. *Plethodon virginia*, Pendleton County, WV, May 2008.

Figure 26. *Plethodon virginia* found on an eastern slope of Heavener Mountain, Pendleton County, WV, March 2008.

Figure 27. Juvenile salamander that may represent a red-striped *Plethodon virginia* or a *Plethodon cinereus* at the base of Heavener Mountain, Pendleton County, WV, March 2008 (previous page).

Figure 28. Female *Plethodon cinereus* guarding eggs attached to a root under a rock in Lost River State Park, Hardy County, WV, June 2008 (following page).

CHAPTER THREE

Multi-model Evaluation of the Patterns of Woodland Salamander Distribution in the Valley and Ridge Physiographic Province

Abstract

Two woodland salamanders, *Plethodon punctatus* and *P. virginia*, are endemic to the Valley and Ridge Physiographic Province in West Virginia and Virginia and occupy limited geographic ranges. Two common and widespread species, *P. cylindraceus* and *P. cinereus*, also inhabit this region. I used two types of modeling to evaluate the distributions of these species with site occupancy data. I used logistic regression to evaluate *a priori* models that were developed with presence-absence data and associated environmental variables from 2008 surveys and ranked them with Akaike's Information Criterion corrected for small sample size (AIC_c). To develop logistic regression models separately for each species, I used presence absence data from all sites where *Plethodon* were detected, which resulted in 71 sites for each species. I then used historic and current presence data to model the distribution of each species with the software program Maxent and WorldClim climatic variables. The output of Maxent models produces a map of each species' potential distribution. To compile current occurrence data, I used daytime cover object searches and nocturnal visual encounter surveys. Geographic locations were recorded with a GPS receiver. Environmental data including substrate type, elevation, ambient temperature, soil temperature and relative humidity were recorded and used in logistic regression modeling. Logistic regression modeling revealed that *P. punctatus* and *P. cinereus* had positive associations with elevation, *P. virginia* was negatively associated with relative humidity, and *P. cylindraceus* occurrence was negatively associated with elevation and positively associated with ambient temperature and relative humidity. Maxent distribution models were evaluated and suggested that the distributions of woodland salamanders are likely shaped by both climatic factors as well as biological factors, possibly in the form of competition.

Introduction

Terrestrial woodland salamanders of the genus *Plethodon* have been the focus of much research about patterns of species co-occurrence, distributional patterns, and competition (Dunn 1926; Grobman 1944; Highton 1972; Hairston 1987; Adams 2007). The idea that similarly sized *Plethodon* species tend to have largely parapatric distributions, while differently sized species co-occur more frequently has been observed and subsequently evaluated as two size-guilds, comprised of a small *Plethodon* guild and a large *Plethodon* guild in which members of a guild tend to occupy similar niches within their ranges (Grobman 1944; Highton 1972; Hairston 1987; Adams 2007; Bruce 2009). Because of these similar niche requirements, similar species tend to not co-occur, while differently sized species tend to co-occur due to the lack of niche overlap. Grobman (1944) described overlapping ranges of differently sized salamanders as “geographical equivalents,” and referred to two such salamander species as “syngeographs.” The largely parapatric arrangement of distributions of similarly sized woodland salamanders has led to investigations into the mechanisms that cause such patterns.

Several studies have evaluated the role of competition and niche partitioning in the patterns of parapatric and sympatric species within size classes, and have suggested that interspecific aggression and territoriality have had a major role in interference competition leading to the exclusion of species (Jaeger 1981; Nishikawa 1985; Jaeger et al. 2002), though the resource at the center of such competition is not always clear (Hairston 1987). Similarly sized woodland salamanders that have broad distributional overlap may not compete as strongly for resources (Hairston 1987), which may be due to the abundance of resources, such as space and food, combined with density independent causes, such as climatic factors that limit the size of populations, thereby reducing competition (Dumas 1956). Adams (2007) found non-random patterns of co-occurrence that supported the hypothesis that two size guilds occurred in eastern *Plethodon* that represented a competitive-based community assemblage in a study that included 45 species of eastern *Plethodon* at 4540 historic sites. Throughout the many studies that have investigated interspecific interactions between woodland salamanders, no one factor has emerged as a primary cause for such patterns of distribution, but causes appear to be specific to particular regions that have unique species assemblages, and combinations of environmental factors such as climate, heterogeneous topography, vegetation, and disturbance history.

Two endemic species of the genus *Plethodon* inhabit the Valley and Ridge Physiographic Province in West Virginia and Virginia. This study focuses on the range of these two endemic species, *Plethodon virginia* (Shenandoah Mountain Salamander) and *Plethodon punctatus* (Cow Knob Salamander). *Plethodon virginia* is limited to Pendleton, Hardy, Grant, and Hampshire counties in West Virginia, and western Rockingham County, Virginia. *Plethodon punctatus* is found in Pendleton, Hardy and Hampshire counties in West Virginia and Augusta, Highland, Rockingham, and Shenandoah counties in Virginia. The two remaining *Plethodon* species that inhabit this range, *P. cylindraceus* (White-spotted Slimy Salamander) and *P. cinereus* (Eastern Red-backed Salamander) are more common and have widespread distributions.

Plethodon punctatus is a medium-large salamander that is restricted to high elevations within a narrow range that is represented by a core distribution along the ridge of Shenandoah Mountain on the Virginia-West Virginia border as well as a few disjunct populations on the relatively high-elevation ridges of Jack Mountain in Pendleton County, WV (Graham, 2007), Nathaniel Mountain in Hampshire county, and Great North Mountain on the border of Hardy County, WV and Shenandoah County, VA (Highton 1972; Flint 2004). Because of its narrow and disjunct range it is a species that is of conservation concern. The West Virginia Division of Natural Resources currently lists *P. punctatus* as an S1 species, which is defined as extremely rare and critically imperiled, while in Virginia, *P. punctatus* is listed as an S2 species (very rare and imperiled) by the Virginia Department of Conservation and Recreation. Globally, *P. punctatus* is listed as a Near Threatened on the International Union for the Conservation of Nature (IUCN) Red List (www.iucnredlist.org), and is listed as a G3 (vulnerable) species by NatureServe due to a small range, high local abundance, and vulnerability to deforestation (www.natureserve.org).

Plethodon virginia is a small eastern *Plethodon* that inhabits wooded slopes and ridges within a narrow section of the Valley and Ridge. No studies have focused on the ecology and natural history of *P. virginia* since its description in1999 when Highton split *P. virginia* from what is now considered its sibling species, *P. hoffmani* (Valley and Ridge Salamander) based on allozyme data from electrophoretic protein comparisons. *Plethodon virginia* was studied when it was still considered *P. hoffmani* prior to 1999 (Fraser 1976a, b) and *P. richmondi* before 1972 (Highton and Jones 1965) when *P. hoffmani* was initially described (Highton 1972). *Plethodon virginia* is listed as an S2 species in both West Virginia and Virginia and G2G3Q globally (where Q denotes questionable taxonomy) by NatureServe and as Near Threatened by the IUCN.

Thus, there are two pairs of similarly sized species within the area of focus. *Plethodon cinereus* and *P. virginia* represent two small *Plethodon* and *P. cylindraceus* and *P. punctatus* are two large *Plethodon*, although *P. punctatus* is noticeably smaller than *P. cylindraceus* and may be considered to be of intermediate size (Green & Pauley 1987; Petranka 1998). Fraser (1976a) investigated the possibility of competition between adult *P. virginia* (then *P. hoffmani*) and juvenile *P. punctatus,* to determine if differently sized salamanders may compete when they overlap in size at particular life stages. The results suggested that variability in seasonal activity patterns between species, and staggered feeding schedules within species largely prevented competitive exclusion from occurring. The interspecific interactions between the species of this area have otherwise not been studied besides observations on the distributions of the species (Highton 1972, 1999; Pauley 1995, 1998; Tucker 1998; Flint 2004; Graham 2007). Highton (1999) suggested that *P. virginia* may be better adapted to the xeric conditions of the Valley and Ridge than *P. cinereus,* which have largely parapatric distributions, and are rarely found together. *Plethodon punctatus* and *P. cylindraceus* have overlapping ranges, but *P. punctatus* is limited to high elevations, while the distribution of *P. cylindraceus* is widespread throughout the area, though is less commonly found at high elevations. Because *P. virginia* and *P. punctatus* are endemic to small ranges, information about their distribution, ecology, and interactions with other species are important for their proper management.

To characterize the distributions of these four species I used two methods of modeling. First, I evaluated species occurrence with AIC model selection of logistic regression models of presence and absence data with environmental and topographic variables from 2008 surveys. I then used species distribution modeling with both current and historic presence data. While logistic regression models and model selection aim to highlight the variables and their combinations that most successfully predict the occurrence of a particular species, the goal of distribution modeling is generally to map the potential distribution of species based on some set of parameters, which are usually some set of abiotic environmental variables. There has been some debate as to whether species distribution modeling, also called ecological niche modeling, produces an output that illustrates a species' realized niche or its fundamental niche (Soberon & Peterson 2005; Araujo & Guisan 2006). While distribution modeling typically estimates ranges based on abiotic environmental variables, biotic factors such as the influence of potential competitors or mutualists are inherently and implicitly incorporated into the models (Araujo & Guisan 2006). Because the exclusion of a species due to the presence of a competitor will influence the distribution of that species, the abiotic variables that coincide with its presence will characterize its modeled distribution even if that species could tolerate and thrive in adjacent ranges where they are absent. It seems likely then, that species distribution models will inherently illustrate something that resembles a realized niche of a species rather than the fundamental niche as defined by Hutchinson (1957).

The objectives of this study were 1) to establish baseline data on the distribution, habitat, and associated environmental variables of woodland salamanders in the Valley and Ridge of West Virginia with emphasis on the endemic species: *P. virginia* and *P. punctatus*, 2) to evaluate patterns of distribution through the development of competing models of species occurrence for woodland salamanders with environmental and topographic explanatory variables at the site level from 2008 surveys, 3) to use current and historic sites to model the distributions of each species based on prevailing climatic data with GIS and distribution modeling software, and 4) to use the resulting information to evaluate distributional patterns of species distributions and occurrence and to develop testable hypotheses to help guide future research.

Methods & Materials

Site Surveys

I surveyed for woodland salamanders at 98 sites within the Valley and Ridge Physiographic Province from March to November 2008 using daytime cover object searches and nighttime visual encounter surveys (VES) during or immediately following rain events (Crump & Scott 1994). Daytime cover object surveys consisted of one to two person-hour surveys in which I turned over natural cover objects, primarily rocks and logs, to locate and record salamanders and environmental data. I used VES primarily in plots with very rocky substrates that consisted of talus slopes and slopes with numerous rocky outcrops. Daytime cover object searches are not effective in detecting salamanders in rocky substrates, while VES during wet nights when salamanders may be active on the surface tend to result in higher rates of detection (Crump & Scott 1994, Flint & Harris 2005). I conducted surveys in areas that represented typical habitat of woodland salamanders, which includes forest habitat with some form of natural cover, such as rocks, leaf litter, and woody debris (Welsh and Droege 2001, Wyman 2003). I selected sampling plots in a non-probabilistic manner because of the limited time, resources, and exploratory nature of this study. Because the distribution and ecology of *P. virginia* has not been studied since its description by Highton (1999), I chose a sampling scheme that allowed maximum coverage of the study area to establish baseline occurrence information for this species. To reduce bias from nonrandom purposive plot selection, I surveyed areas that represented the topographic heterogeneity of the area (i.e., aspect, slope, elevation), and across the study area geographically and temporally (i.e. March-November).

Upon detection I hand-captured and identified salamanders and placed them in plastic zip-sealed bags to be measured on-site and recorded the geographic locations of each site with a Garmin GPS60 receiver. I measured snout-vent length (SVL) from the anterior end of the snout to the posterior end of the cloaca, tail length from the posterior end of the cloaca to the tip of the tail, and cranial width at the widest part of the jaw. I used spring scales to measure mass. Upon completion of measurements, salamanders were released at the point of capture.

Habitat and Environmental Parameters

I took data on environmental parameters at each site that was surveyed. I recorded relative humidity and ambient temperature of the exact location of capture by placing a thermo-hygrometer on the surface at which each individual was located. I measured soil temperature with a digital pocket thermometer that was probed approximately 3 cm into the soil at or within the immediate vicinity of the location of each individual. I recorded cover object type (rock, log) and characterized the substrate in which each individual was located with a ranking system based on rockiness and depth of soil. I developed a substrate-ranking system adapted from similar substrate-classification schemes by Jaeger (1970, 1971, 1980) and Fraser (1976a). Jaeger (1970) classified three types of talus slopes based on the ratio of rock to soil and organic mater where: Type I = bare rocks with no soil, Type II = rocky substrate with limited soil and significant humus accumulation, and Type III = talus at base of slope with significant soil accumulation, fewer exposed rocks. Fraser (1976a) ranked substrate from 1-5 based on the volume of space directly beneath cover objects where 1 = a rock that was "closely adpressed to the ground," and 5 = a large rock with a large amount of space underneath. I developed a scheme where substrate within the immediate vicinity of individual salamanders was scored based on the relative amounts of rock, space, soil, and humus beneath the cover object for daytime cover object searches and directly below the point of capture in VESs. In this scheme, 1 = a rocky substrate with no soil or humus, and only space between and beneath rocks, and 5 = deep soil with few to no rocks. All scores recorded ranged from 1.5 (very rocky with shallow soil deposits) to 4 (deeply packed soil among rocks, with few to no exposed rocks).

Logistic Regression Analysis

I used logistic regression to develop maximum likelihood models for each species with salamander presence or absence as the binary response variable and the environmental and physical data collected as explanatory variables. Because sites were the sampling units used for comparison, I obtained the mean of each explanatory variable from woodland salamander presence points within each site for analysis. Prior to analysis, I tested for collinearity between the explanatory variables to identify and remove any redundant variables (Pearson's $r \geq 0.70$). I used the remaining four variables to develop six *a priori* models for statistical analyses based on review of natural history and habitat requirements of woodland salamanders from literature and evaluation of different combinations of environmental and physical characteristics (Tables 11 & 12). I included all variables in a global model to assess goodness-of-fit (Burnham & Anderson 2002). I employed the same 6 models for each of the species separately with the same 71 sites and environmental data.

With some exceptions, a distance of greater than 50 m separated sites that were included in logistic regression analysis. Three sites included in analyses were visited twice, and are represented as separate sites in regression analysis because environmental conditions were different in each repeated survey. Because sites were generally visited only once, I was unable to account for detection probability. As a result, sites that represent absence in regression analysis may not indicate true absence, and instead represent the failure to detect a species.

I used Akaike's Information Criterion (AIC_c) for model selection. Because the number of sites included in analysis (n = 71) was relatively small compared to the number of parameters (K) used to develop models (i.e., $n/K \leq 40$) I used AIC corrected for small sample sizes (AIC_c) for model comparison (Burnham & Anderson 2002). I ranked candidate models based on their calculated AIC_c values where lower values represent a more parsimonious and therefore stronger model (Burnham and Anderson 2002). I used models with AIC_c values within 2 units of the most parsimonious model to draw inferences for each species (Burnham & Anderson 2002).

Species Distribution Modeling

To model the distribution of each salamander, I used the software program Maxent version 3.2.19 (Phillips et al. 2004), which uses presence-only data to model species distributions with some set of environmental variables in raster data layers under the principles of maximum entropy. Phillips et al. (2004) summarized maximum entropy in this context as an estimated probability distribution with maximum uniformity constrained by the empirical averages of each feature (i.e. environmental variables) throughout the geographical area of interest, and likened its output to a maximum-likelihood distribution of a species. To develop models for each species, I compiled presence data from 2008 surveys, the Marshall University Herpetology Museum, past studies on the species (Pauley 1995, 1998, Tucker 1998, Graham 2007), and from the Division of Amphibians and Reptiles of the National Museum of Natural History (USNM). Presence data were collected from Pendleton, Hardy and Hampshire counties, WV and Highland, Augusta, Rockingham, and Shenandoah counties, VA (Table 22). Maxent uses random background points within the projected geographical area to represent the range of environmental variables within the area and provides a reference to suitable habitat of the species being modeled. I used the default 10,000 background points. The environmental variables used were climatic variables from the WorldClim database (Hijmans et al. 2005), which are freely available on the internet (www.worldclim.org). WorldClim data layers are based on average monthly precipitation and temperature data from 1960-1990 and are presented in raster format at a 1-km^2 resolution worldwide (Hijmans et al. 2005). To reduce over-parameterization, a model was developed for each species in which all climatic variables were used and reduced to the six variables that contributed most to each model based on a jackknifing procedure and percent contribution (Tables 23-26), both of which are provided within the Maxent output. To determine what effect one species distribution may have on the modeling of another, I used the modeled probability distribution output from similarly sized *Plethodon* as an additional variable in a separate model of its counterpart's modeled distribution. The resulting output within Maxent provides response curves for each continuous variable against the probability of occurrence based on the environmental variables. To reduce autocorrelation, I chose to allow only one presence point per km^2 cell to be included in analyses.

Results

From March through November 2008, 321 woodland salamanders were recorded at 91 sites including 74 *P. punctatus* at 23 sites, 48 *P. virginia* at 33 sites, 112 *P. cinereus* at 22 sites and 73 *P. cylindraceus* at 38 sites; 25 sites had more than one species. Because *P. virginia* has a zone of hybridization with a sibling species, *Plethodon hoffmani*, at the southern extent of its range and the two species are indistinguishable in external characteristics (Highton 1999), sites located within the vicinity of Reddish Knob in Pendleton County (sites: n = 6; individuals: n = 14) possibly represent occurrence of hybrids and were not included in analyses.

Regression analysis

Statistical analyses included data from the 71 sites that had complete environmental data. Because soil temperature and elevation were found to have a negative linear relationship (Pearson's $r < -0.7$), soil temperature was not included in the candidate models.

The ambient model received the most support among the candidate models in assessing occurrence of *P. virginia* (Table 13). Relative humidity had a negative relationship with occurrence of *P. virginia*, (Table 14). Both the elevation and physical models received support in the case of *P. punctatus* (Table 17), for which elevation had a positive relationship with *P. punctatus* occurrence (Table 18). The global model ranked highest for *P. cylindraceus* (Table 19), in which air temperature and relative humidity had a positive relationship, while elevation had a negative relationship with occurrence (Table 20). Both the elevation and physical models received support for *P. cinereus* (Table 15); elevation had a positive relationship with occurrence (Table 16).

When Akaike weights (w_i) were summed among models for each species to evaluate the relative importance of each explanatory variable (Table 21), elevation had the greatest weight for *P. punctatus, P. cylindraceus,* and *P. cinereus*. Air temperature had the greatest summed weight for *P. virginia*. It is important to point out that all of the explanatory variables except for relative humidity were included in three of the candidate models while relative humidity was included in only two models. Because of this, the sum of Akaike weights is not balanced between the variables. If, instead, an average weight of each explanatory variable had been taken, relative humidity could have had the greatest average weight for *P. cylindraceus* and *P. virginia*. I did not develop a relative humidity-only model because relative humidity is meaningless without temperature.

Species Distribution Modeling

The species distribution models for *P. virginia* (Figure 29) and *P. punctatus* (Figure 33), the two endemic species, produced maps that showed distinct ranges, while the *P. cinereus* range map was more scattered and less distinct (Figure 31). The *P. cylindraceus* map had a distinct and widespread area of high probability of occurrence (Figure 35). Because the vast majority of the data collected came from public lands (*e.g.*, George Washington National Forest) within the mountainous area of the Valley and Ridge, the resulting maps showed similar southwest to northwest patterns that followed the characteristic long parallel ridges and valleys of the Valley and Ridge. While the output provided plausible maps for *P. punctatus* and *P. virginia*, the known ranges of *P. cinereus* and *P. cylindraceus* extend well beyond the area considered, and sampling bias likely plays a part in their maps that show a more limited range of suitable habitat.

Each species had a unique set of variables that were considered most important from jackknife and percent contribution results. However, *P. cylindraceus* and *P. cinereus* had the same variable that contributed most, precipitation in the wettest month (Figures 25 & 27). *Plethodon virginia* and *P. punctatus* models also included precipitation of the wettest month, but in each case, it was the second most important variable. The most important variable in the *P. virginia* model was mean temperature of the warmest quarter, while the most important variable for *P. punctatus* was maximum temperature in the warmest month (Figures 24 & 26).

Models for each species with a seventh environmental variable consisting of the distribution model of the similarly sized potential competitor produced output maps that were very similar to the six-variable models. Response curves illustrated the change in a species' probability of occurrence as another species probability of occurrence changes (Figures 37-40). In each case, there was a response curve in which the seventh variable (competitor's probability of occurrence) changed while the six remaining variables remained at their average value, and therefore showed the seventh variable's marginal effect (Figures 37 & 39), as well as a response curve for the seventh variable as the sole variable considered in the model (Figures 38 & 40).

Discussion

Small Plethodon

The distribution and patterns of occurrence of woodland salamanders in the Valley and Ridge Physiographic Province has been studied and discussed as a function of both competition (Fraser 1976b) and adaptation to climatic regimes (Highton 1972, 1999). Highton (1972, 1999) speculated that *P. cinereus* is largely absent from a substantial portion of the relatively hot and dry climate of the Valley and Ridge, where *P. virginia* and *P. hoffmani* may be better adapted due to greater body size (Fraser 1976b) and smaller clutch size (Angle 1969). Jaeger (1971) found that *P. shenandoah*, also a larger salamander than *P. cinereus*, was likely better adapted to the hotter, drier microclimate of talus slopes where *P. cinereus* was more susceptible to desiccation. *Plethodon cinereus* was more common in the cooler and moister microclimates of the deeper soil around the talus slopes where Jaeger suggested *P. shenandoah* was largely absent due to the competitive superiority of *P. cinereus*. In this study, the ambient model, which aimed to include parameters that described the microclimate, was the best model for *P. virginia* (Table 13). The negative relationship of relative humidity in predicting *P. virginia* occurrence from the logistic regression model is consistent with the speculations of Highton (1999) (Table 14).

The strength of weight of elevation in the logistic regression models for *P. cinereus* is consistent with patterns observed in the field (Table 16). *Plethodon cinereus* was located largely at high elevations on Shenandoah Mountain. However, it is important to note that *P. cinereus* was also found at lower elevations as well, though at fewer sites. From observations in the field, *P. cinereus* occupies narrow areas within the region of interest along the ridges of the high elevations (1030-1350 m) of Shenandoah Mountain at 11 sites, or in lower elevations (560-750 m) in valleys and coves in five sites in the northern area of *P. virginia*'s range in Hampshire and northern Hardy counties. One site, on Helmick Rock in Hardy County, WV is a relatively high elevation site (880 m) where *P. punctatus* was also found. All remaining sites where *P. cinereus* was found in 2008 surveys are outside of the known range of *P. virginia*. By contrast, *P. virginia* tends to inhabit the drier slopes of Shenandoah Mountain as well as high elevations along the ridge, and were the only woodland salamanders found on the drier ridges that run parallel to the west of Shenandoah Mountain.

The Maxent species distribution models for *P. virginia* and *P. cinereus* result in two contrasting maps. The map for *P. virginia* is a clearly defined range that may be a plausible actual range of the salamander. This map only excludes occurrence data from the far western edge of its range, which are each just east of the South Branch of the Potomac River, and at one location at the far northern extent of its range where more surveys may be warranted (Figure 29). One area where *P. virginia* has not been recorded and shows a high suitability is in the vicinity of Great North Mountain in Hardy County. Highton (1999) suggests that the Cacapon River, (Lost River directly west of Great North Mountain) is a likely boundary to *P. virginia*. The area of greatest overlap appears to be along the ridgeline of Shenandoah Mountain and the area to the immediate east in Virginia, where both species have been found. In the output map for *P. cinereus*, the suitability of habitat appears to quickly decline west of the ridge of Shenandoah Mountain (Figure 31), while the modeled *P. virginia* suitability remains strong. Within this general area, except in far south Pendleton County, *P. cinereus* has not been found between the South Branch Potomac River and the ridge of Shenandoah Mountain, where *P. virginia* has been found and shows the widest area of relatively suitable habitat. It would appear that in this region, *P. virginia* excludes *P. cinereus*. Conversely, there appears to be overlap to the east of Shenandoah Mountain and in the northern part of *P. virginia*'s range.

The response curves for these salamanders when the potential competitor's distribution model is used as a seventh variable illustrate the nature of the ranges of the two salamanders, with *P. virginia's* range being characterized as restricted geographically and *P. cinereus* as the more widespread species (Figures 37 & 38). The overall shapes of the curves are somewhat similar to the curves for *P. punctatus* and *P. cylindraceus*, also characterized by one restricted range (*P. punctatus*) and one widespread range (*P. cylindraceus*) (Figures 39 & 40). However, the response curve of *P. cinereus* that displays the change in suitability across the suitability of *P. virginia*, with all other variables at their respective average (Figure 37b), shows an extreme decline in *P. cinereus* suitability with increasing *P. virginia* suitability. This would suggest that in otherwise suitable habitat (i.e. the 6 original variables at their average values), areas where *P. virginia* are well suited are relatively poorly suited for *P. cinereus*. The fact that *P. virginia* is restricted to the relatively hot and dry area of the Valley and Ridge, while *P. cinereus* can be found outside of this range, implies that either *P. cinereus* is less well adapted to such climatic conditions, or that the presence of *P. virginia* precludes the presence of *P. cinereus* (Figure 37b).

The response curve of *P. virginia* distribution, with *P. cinereus* probability of occurrence as the seventh variable (Figure 37a), shows very low suitability for *P. virginia* in areas where the *P. cinereus* model shows low to moderate suitability. This is expected because the modeled and actual distribution of *P. cinereus* extends well outside of *P. virginia's* distribution, where *P. cinereus* showed low to moderate suitability. *Plethodon virginia's* probability of occurrence rises steeply where *P. cinereus* has a higher probability of occurrence. Because *P. virginia* was found in areas where *P. cinereus* had a high probability of occurrence, such as the area along Shenandoah Mountain, this response curve shows a positive association. The response curves in which potential competitors' distribution models are the sole variable used both show positive relationships, but with different shapes (Figure 38). The trend suggests that low to moderately suitable habitat for *P. cinereus* is poorly suited for *P. virginia*, while poorly suitable habitat to *P. virginia* is suitable to *P. cinereus*. This is likely a function of the widespread distribution of *P. cinereus* across climatic regimes throughout the area compared to the restricted distribution of *P. virginia*. The important distinction between the two sets of curves is that one set shows the change in a potential competitor's suitability while other environmental variables are held constant, which constrains the resulting curve to suitable habitat based on the other six environmental variables because those values being held constant are averages from presence localities. Curves showing only the potential competitor's probability of occurrence do not factor in the other six environmental variables, and are therefore less constrained.

Past studies into the relationships of similarly sized woodland salamanders have found comparable patterns of limited co-occurrence, and have investigated sympatric and allopatric populations. Morphological character displacement was found to occur between *P. cinereus* and *P. hoffmani* in which *P. hoffmani* has apparently become better adapted in exploiting larger prey items than *P. cinereus* when the two species occur in sympatry (Adams & Rohlf 2000). Jaeger et al. (2002) investigated interspecific aggression between *P. cinereus* and *P. hoffmani*, and found that *P. cinereus* is the more aggressive and territorial salamander. They suggested two possible conclusions about the narrow area where the distributions of the two species are largely parapatric. First, *P. cinereus* is possibly expanding its range into the range of *P. hoffmani* because it is superior in aggressive interspecific interactions and second, that contact boundaries may be static if *P. hoffmani* is exploitatively superior in foraging, which could counteract the aggressive superiority of *P. cinereus*. However, they do not account for the fact that the larger body size and smaller clutch size of *P. hoffmani* may make it better adapted to the hotter, drier climate of the Valley and Ridge (Highton 1972, 1999), which could be another possible explanation of a relatively static parapatric contact zone between the two species. Woodland salamanders have been found to partition habitat based on moisture regimes (Jaeger 1971; Pauley 1978), so it is possible that these two species may be able to coexist with overlapping ranges that provide heterogeneous conditions that allow them to avoid competition and to only rarely co-occur. *Plethodon virginia* appears to have a similar relationship with *P. cinereus* as *P. hoffmani*; their distributions are largely parapatric, and *P. virginia* is more widespread in the relatively xeric ridges and slopes of the Valley and Ridge. If *P. cinereus* is the more successful aggressive competitor, but *P. virginia* and *P. hoffmani* are better adapted to xeric conditions, the invasion of one species into the range of another is likely to depend largely on climate. The fact that the range of *P. cinereus* surrounds the ranges of *P. virginia* and *P. hoffmani* would suggest that it may be encroaching on their historic ranges. However, this could also be an artifact of past climates, and with current changes in climate towards warmer conditions, it is possible that the encroachment has slowed or even the reversed, and the range of *P. cinereus* could be receding in the Valley and Ridge. More long-term climatic and occupancy data are needed to investigate this reasoning. The use of environmental data-loggers used in a probabilistic sampling scheme at *P. cinereus* and *P. virginia* sites would likely produce more definite results regarding the adaptation of *P. virginia* and *P. hoffmani* to more xeric climatic conditions. The use of GIS to evaluate the topography of *P. cinereus* and *P. virginia* presence sites could analyze topographic features (aspect, slope, elevation, curvature) which can provide information on important climatic variables such as insolation, which can have an effect on microclimate, and habitat partitioning (Pauley 1978).

Large Plethodon

The elevation model was not surprisingly the best for *P. punctatus* (Table 17), which is typically found above 950 m, though has been found at 732 m (Buhlmann et al. 1988). Though substrate was the only other variable that contributed to supported models, confidence intervals were too wide to infer statistical support for the negative relationship according to parameter estimates and odds ratios (Table 18). However, past studies and reports in literature (Green & Pauley 1987; Buhlmann et al. 1988; Flint & Harris 2005) as well as implications from surveys in the current study suggest that there is a strong correlation between *P. punctatus* and rocky substrates such as talus that are associated with rock outcrops. Because the substrate was evaluated only within the immediate vicinity of the salamander captured, and not on the overall substrate across a representative population, the substrate value given may be more dependent on the greater ability to detect individuals in areas with deeper soil and less space between rocks. In daytime cover object surveys, *P. punctatus* are easier to detect in areas of deeper soil that surround areas of talus (Flint & Harris 2005). Because relatively fewer nighttime surveys in areas of talus were conducted where *P. punctatus* was found in very rocky substrates (i.e. substrate = 1.5), the values are not likely to be representative of true associations. Measures of distance from a talus slope or a subjective characterization of the overall habitat of a wider area (i.e. across the plot surveyed) would likely have been more representative of the association of *P. punctatus* with rocky substrates.

The global model received the most support in the case of *P. cylindraceus* (Table 19), which is likely because three of the four parameters had statistically-supported effects on the prediction of occurrence (Table 20). Based on field observations, *P. cylindraceus* appears to be the most widespread species in the region. While *P. cylindraceus* occupies all elevations in the area, it appears to be more common at lower elevations, a finding that this model supports. This salamander also appears to be especially common in valleys and ravines that are often within the vicinity of streams, which may account for the positive effect of relative humidity on occurrence, though *P. cylindraceus* were also found less commonly on drier slopes and ridges. *Plethodon cylindraceus* was the only salamander to have a statistically supported positive effect of air temperature on occurrence, which is likely because it was the most commonly located salamander in the warm summer months.

Distribution maps produced with Maxent models show clearly the restricted nature of *P. punctatus* distribution (Figure 33) and the widespread distribution of *P.*

cylindraceus (Figure 35). The modeled range of *P. punctatus* also illustrates the disjunct nature of its range. Areas of high probability that have few occurrence localities, such as South Branch Mountain, Jack Mountain and Great North Mountains may not have been sufficiently sampled to determine the extent of *P. punctatus's* distribution, and may be under-sampled because much of the land is privately owned (Pauley 1998, Graham 2007). Other areas that show high suitability where *P. punctatus* has not been found and may be under-sampled are Simmons Mountain, Panther Knob, Ruleman Mountain, and other peaks in their vicinity, which are all located to the west of Jack Mountain in western Pendleton County. The remaining area that shows high suitability is to the northwest of the Jack Mountain site near Dickinson Mountain and the associated knobs and ridges. Conversely, *P. cylindraceus* are distributed throughout the area, which is illustrated clearly in its modeled distribution.

The response curves of *P. punctatus* and *P. cylindraceus* are indicative of a widespread species and a highly restricted species, but the curve for *P. cylindraceus* does not show a distinct drop-off in suitability with increasing *P. punctatus* suitability as *P. cinereus* showed with *P. virginia*, but instead continues to rise (Figures 39 & 40). *Plethodon punctatus* shows a slight drop in suitability across high *P. cylindraceus* suitability. As expected, low *P. punctatus* probability of occurrence shows a high level of suitability for *P. cylindraceus*, while only high probability areas for *P. cylindraceus* appear suitable for *P. punctatus*. In this case, both types of response curves (with and without the six environmental variables included) for each species are similar. This is likely because *P. punctatus* does not exclude *P. cylindraceus* from any considerable amount of geographical space as *P. virginia* does with *P. cinereus*. However, *P.*

cylindraceus is much less common in the narrow region of the higher elevations of Shenandoah Mountain where *P. punctatus* is relatively common. This high elevation region is considerably cooler and moister relative to the general hot and dry climate of the Valley and Ridge. The question then is does *P. cylindraceus* prevent *P. punctatus* from expanding its range due to competitive pressure or is *P. punctatus* poorly adapted to the predominately hot and dry Valley and Ridge?

While *P. cylindraceus* is found at all elevations, it seems to be associated with the relatively lower elevations within the area. The tendency for large *Plethodon* to be separated altitudinally is not uncommon. Hairston (1949) found that *P. cylindraceus* and *P. metcalfi* were largely separated altitudinally in the Black Mountains of North Carolina, where *P. metcalfi* occupies high elevations. Subsequent studies (Hairston 1951; Highton & Peabody 2000) showed that salamanders of the *P. jordani* group that occur at high elevations in the southern Appalachians tend to replace members of the *P. glutinosus* group, which occur within the same areas but at lower elevations. On mountains where *P. jordani* complex salamanders do not occur, *P. glutinosus* species tend to occupy all elevations (reviewed in Wells 2007). This is not always the case. For instance, in the Balsam Mountains of North Carolina *P. metcalfi* (of the *P. jordani* complex) tends to overlap greatly in altitudinal distribution with *P. teyahalee* (of the *P. glutinosus* complex) (Hairston 1980). Nishikawa (1985, 1987) found that *P. jordani* and *P. teyahalee*, which had little elevational overlap in the Great Smoky Mountains, showed more interspecific aggression than *P. metcalfi* and *P. teyahalee* from the Balsam Mountains which were consistent with Hairston's findings that competition for resources drove such patterns of distribution (Hairston 1980). Marvin (1998) found that two widely sympatric species, *P.*

glutinosus and *P. kentucki* were both equally aggressive to conspecifics as they were to heterospecific individuals, and that *P. glutinosus* was the superior aggressor. While *P. cylindraceus* and *P. punctatus* have been found syntopically (Mitchell and Pauley 2005), and were found together at two sites in this study, it is clear that they do not commonly co-occur. Because *P. punctatus* tends to inhabit high elevation areas within talus at the highest densities (Flint & Harris 2005), while *P. cylindraceus* is more commonly found at lower elevations and seems to inhabit a wider variety of substrates, niche partitioning, character displacement, and aggressive interactions should be investigated to provide insight into their ecological relationship. Co-occurring *P. glutinosus* and *P. wehrlei* (a sibling species of *P. punctatus*) to the Alleghenies in West Virginia could be used to investigate interspecific reactions across species complexes and physiographic provinces. Whether the disjunct and limited elevational distribution of *P. punctatus* is partially a factor of interspecific interactions may be difficult to determine based on environmental and distributional data alone. Buhlmann et al. (1988) suggest that one possible reason for the disjunct distribution and talus-specific habitat of *P. punctatus* is the repeated timber harvesting throughout much of its range in the early 20th century. Human disturbance within the area likely has an effect on the distribution of these salamanders as has been shown in other woodland salamanders (Petranka et al. 1993; Marsh & Beckman 2004, Pauley 2008).

Conclusions

Because the logistic regression aspect of this study was exploratory and sites were visited only once, caution must be used in interpreting the results. However, the results are likely to be useful in designing future studies that investigate the mechanisms that drive the apparent patterns of distribution of woodland salamanders in the Valley and Ridge. With information on the distribution of these species, future studies should select sites in a probabilistic manner and visit them multiple times in a season to account for imperfect detection to develop reliable estimates of habitat associations and population and relative abundance parameters (Hyde & Simons 2001, 2005; MacKenzie et al. 2002; Bailey et al. 2004). It is also important to consider that parameters such as relative humidity and ambient temperature are dependent on the day and time measurements are taken, and generally have an impact on whether a species is active or inactive. I conducted surveys regardless of the weather conditions in daytime cover object surveys, and after or during rains for VESs. *Plethodon virginia* and *P. cylindraceus* occurrence were found to be affected by these ambient variables. Because relative humidity and temperature are important in the activity patterns of woodland salamanders in general, and this study included only sites where woodland salamanders were present, I believe that the associations with relative humidity and temperature are not only a function of seasonal and daily activity, but on site characteristics that affect long-term microhabitat conditions as well. Afore-mentioned suggestions for monitoring of salamanders and environmental parameters will likely result in estimates that can be interpreted with greater confidence.

The results of this study are consistent with the past observations that similar-sized woodland salamanders tend to have parapatric distributions (Grobman 1944; Highton 1972; Adams 2007), though they do not allow me to suggest whether interspecific competition is the cause of this apparent distribution pattern in the Valley and Ridge. While the Valley and Ridge is a hotter and drier area compared to surrounding physiographic provinces (Highton 1972; Strausbaugh & Core 1978), further studies are needed to investigate whether *P. virginia* is better suited for such a climate than *P. cinereus*, or if *P. cinereus* is likely encroaching on the range of *P. virginia*. If populations of *P. cinereus* on the ridge of Shenandoah Mountain and elsewhere in the Valley and ridge are isolated in moister areas, then it would seem more likely that *P. cinereus* is only able to maintain territory in areas of greater moisture, and its apparent superiority in aggressive interactions with similar-sized *Plethodon* allow those populations to persist. The existence of isolated *P. cinereus* populations may be a result of major climatic fluctuations over the past millions of years that have likely driven evolution and in part shaped distributional patterns of woodland salamander distribution (Highton 1972, 1995, 1999; Hairston 1987; Kozak & Weins 2006) and may be an indication of past invasions of *P. cinereus* into the Valley and Ridge. However, if the *P. cinereus* populations within the range of *P. virginia* are continuous with outside populations, there may be evidence that *P. cinereus* is expanding its range into the Valley and Ridge. Future studies should employ long-term monitoring of sympatric and allopatric populations of *P. virginia* and *P. cinereus* along with environmental variables to characterize their habitat with a specific focus on climatic factors. Aggression trials (Jaeger et al 2002), reciprocal transplants (Cunningham et al. 2009), and other ecological experiments into species interactions and environmental tolerance could provide insight into what shapes species distributions in this region.

Interspecific interactions between *P. cylindraceus* and *P. punctatus* should also be investigated with competition experiments that include other salamanders from their species complexes (i.e. *P. glutinosus* and *P. wehrlei*) to evaluate differences in behavior between populations that overlap in elevational distribution and populations that do not appear to overlap. Because *P. punctatus* has such a limited and disjunct distribution, it is a species of particular concern, and information on the mechanisms that limit its distribution is important for management of the species. *Plethodon virginia* is a species that has only recently been described (Highton 1999), and also has a limited range, so information on its distribution and ecology are important to establish a baseline for future studies and management.

Table 11. Variables measured at the 71 *Plethodon* occurrence sites included in logistic regression analysis in 2008 surveys.

Variable	n	Abbrev.	Mean	SD	Min	Max
Air temperature (°C)	71	AT	19.1	4.7	10.9	30.0
Relative humidity (%)	71	RH	68.4	22.8	32.0	100.0
Elevation (m)	71	EL	842.9	212.3	536	1310
Substrate*	71	SU	2.55	0.5	1.5	4.0

*Substrate is an interval variable (at intervals of 0.5) where 1=rocky substrate with no soil and 5=deep soil with little to no rock.

Table 12. Description and justification of *a priori* regression models.

Model name	**Variables**[a]	**Justification**
Ambient	RH, AT	Microclimatic variables are important to woodland salamander activity, species may be adapted to certain climatic regimes.
Temperature	AT	May be important in woodland salamander activity, species may be adapted to certain temperature regimes.
Physical	EL, SU	Woodland salamander species may be adapted to areas of particular topography and geology.
Elevation	EL	Woodland salamander species may have distributions restricted to particular elevational range.
Substrate	SU	Woodland salamander species may be adapted to substrate types concerning ratio of rocks, interstitial spaces and soil.
Global	RH, AT, EL, SU	This model is used to assess all variables on woodland salamander occurrence and to test goodness of fit (Burnham and Anderson 2002).

[a] RH = relative humidity; AT = ambient temperature; EL = elevation; SU = substrate type

Plethodon virginia

Table 13. *A priori* logistic regression models, listed in order of parsimony by Akaike's Information Criterion adjusted for small sample size (AIC_C), predicting the presence of *Plethodon virginia* in the Valley and Ridge Physiographic Province in West Virginia, 2008.

Model[a]	-2 log likelihood	K[b]	AIC_C[c]	ΔAIC_C[d]	w_i[e]
Ambient (*AT*, *RH*)	90.34	3	96.73	0.00	0.43
Substrate (*SU*)	94.61	2	98.79	2.06	0.15
Global (*AT*, *RH*, *SU*, *EL*)	88.24	5	99.16	2.44	0.13
Temperature (*AT*)	95.19	2	99.37	2.64	0.12
Elevation (*EL*)	95.23	2	99.41	2.68	0.11
Physical (*SU*, *EL*)	94.56	3	100.92	4.20	0.05

[a] Six candidate models were developed with 4 explanatory variables: AT = ambient temperature, RH = relative humidity, SU = substrate, EL = elevation
[b] Number of parameters included in each model
[c] Akaike's Information Criterion adjusted for small sample sizes
[d] The difference in AIC_C score between the best model and each subsequent model
[e] Akaike weights: probability that a model is the best among all candidate models

Plethodon virginia

Table 14. Parameter estimates (β) and odds ratios of parameters of logistic regression model predicting the presence of *Plethodon virginia* in the Valley and Ridge Physiographic Province of West Virginia. The ambient model was the only model that received empirical support ($\Delta AIC_C \leq 2.00$).

Model	β	SE	Odds ratio[a]	95% CI[b]
Ambient[c]				
RH*	-0.028	0.013	0.973	0.948-0.998
AT	-0.074	0.063	0.928	0.821-1.050

[a] Odds ratios > 1 indicate a positive interaction in predicting presence and odds ratios < 1 indicate a negative interaction
[b] Odds Ratios with 95% confidence intervals that do not include 1.0 have statistical support
[c] Model with most support
*P < 0.05
**P < 0.0001

Plethodon cinereus

Table 15. *A priori* logistic regression models, listed in order of parsimony based on Akaike's Information Criterion adjusted for small sample size (AIC_C), predicting the presence of *Plethodon cinereus* in the Valley and Ridge Physiographic Province in West Virginia, 2008.

Model	-2 log likelihood	K	AIC_C	ΔAIC_C	w_i
Elevation (*EL*)	74.97	2	82.33	0.00	0.60
Physical (*SU*, *EL*)	83.12	3	84.20	1.86	0.24
Global (*AT*, *RH*, *SU*, *EL*)	77.84	5	85.90	3.57	0.10
Temperature (*AT*)	86.52	2	88.15	5.82	0.03
Ambient (*AT*, *RH*)	78.16	3	89.48	7.15	0.02
Substrate (*SU*)	83.98	2	90.70	8.36	0.01

[a] Six candidate models were developed with 4 explanatory variables: AT = ambient temperature, RH = relative humidity, SU = substrate, EL = elevation
[b] Number of parameters included in each model
[c] Akaike's Information Criterion adjusted for small sample sizes
[d] The difference in AIC_C score between the best model and each subsequent model
[e] Akaike weights: probability that a model is the best among all candidate models

Plethodon cinereus

Table 16. Parameter estimates (β) and odds ratios of parameters of logistic regression model predicting the presence of *Plethodon cinereus* in the Valley and Ridge Physiographic Province of West Virginia. Two models received empirical support ($\Delta AIC_C \leq 2.00$).

Model	β	SE	Odds ratio[a]	95% CI[b]
Elevation[c]				
EL*	0.004	0.001	1.004	1.001-1.007
Physical				
EL*	0.004	0.001	1.004	1.001-1.007
SU	-0.295	0.525	0.744	0.266-2.083

[a] Odds ratios > 1 indicate a positive interaction in predicting presence and odds ratios < 1 indicate a negative interaction
[b] Odds ratios with 95% confidence intervals that do not include 1.0 have statistical support
[c] Model with most support
*P < 0.05
**P < 0.0001

Plethodon punctatus

Table 17. *A priori* logistic regression models, listed in order of parsimony based on Akaike's Information Criterion adjusted for small sample size (AIC_C), predicting the presence of *Plethodon punctatus* in the Valley and Ridge Physiographic Province in West Virginia, 2008.

Model	-2 log likelihood	K	AIC_C	ΔAIC_C	w_i
Elevation (*EL*)	42.31	2	46.48	0.00	0.57
Physical (*SU*, *EL*)	40.69	3	47.05	0.56	0.43
Ambient (*AT*, *RH*)	72.43	3	78.79	32.30	0.00
Substrate (*SU*)	83.16	2	87.34	40.86	0.00
Temperature (*AT*)	86.65	2	90.83	44.35	0.00
Global (*AT*, *RH*, *SU*, *EL*)	86.65	5	97.58	51.09	0.00

[a] Six candidate models were developed with 4 explanatory variables: AT = ambient temperature, RH = relative humidity, SU = substrate, EL = elevation
[b] Number of parameters included in each model
[c] Akaike's Information Criterion adjusted for small sample sizes
[d] The difference in AIC_C score between the best model and each subsequent model
[e] Akaike weights: probability that a model is the best among all candidate models

Plethodon punctatus

Table 18. Parameter estimates (β) and odds ratios of parameters of logistic regression model predicting the presence of *Plethodon punctatus* in the Valley and Ridge Physiographic Province of West Virginia. Two models received empirical support ($\Delta AIC_C \leq 2.00$).

Model	β	SE	Odds ratio[a]	95% CI[b]
Elevation[c]				
EL***	0.013	0.003	1.013	1.007-1.019
Physical				
EL***	0.013	0.003	1.013	1.007-1.019
SU	-0.989	0.790	0.372	0.079-1.746

[a] Odds ratios > 1 indicate a positive interaction in predicting presence and odds ratios < 1 indicate a negative interaction
[b] Odds ratios with 95% confidence intervals that do not include 1.0 have statistical support
[c] Model with most support
*P < 0.05
**P < 0.0001

Plethodon cylindraceus

Table 19. *A priori* logistic regression models, listed in order of parsimony based on Akaike's Information Criterion adjusted for small sample size (AIC_C), predicting the presence of *Plethodon cylindraceus* in the Valley and Ridge Physiographic Province in West Virginia, 2008.

Model	-2 log likelihood	K	AIC_C	ΔAIC_C	w_i
Global (*AT*, *RH*, *SU*, *EL*)	50.05	5	60.97	0.00	0.85
Elevation (*EL*)	61.13	2	65.31	4.34	0.10
Physical (*SU*, *EL*)	60.01	3	66.37	5.39	0.06
Temperature (*AT*)	85.42	2	89.59	28.62	0.00
Ambient (*AT*, *RH*)	85.06	3	91.42	30.45	0.00
Substrate (*SU*)	91.10	2	95.28	34.30	0.00

[a] Six candidate models were developed with 4 explanatory variables: AT = ambient temperature, RH = relative humidity, SU = substrate, EL = elevation
[b] Number of parameters included in each model
[c] Akaike's Information Criterion adjusted for small sample sizes
[d] The difference in AIC_C score between the best model and each subsequent model
[e] Akaike weights: probability that a model is the best among all candidate models

Plethodon cylindraceus

Table 20. Parameter estimates (β) and odds ratios of parameters of logistic regression model predicting the presence of *Plethodon cylindraceus* in the Valley and Ridge Physiographic Province of West Virginia. Only the global model received empirical support ($\Delta AIC_C \leq 2.00$).

Model	β	SE	Odds ratio[a]	95% CI[b]
Global[c]				
RH*	0.051	0.022	1.052	1.007-1.099
AT*	0.252	0.105	1.286	1.047-1.580
EL**	-0.012	0.003	0.988	0.982-0.994
SU	0.534	0.650	1.705	0.477-6.099

[a] Odds ratios > 1 indicate a positive interaction in predicting presence and odds ratios < 1 indicate a negative interaction
[b] Odds ratios with 95% confidence intervals that do not include 1.0 have statistical support
[c] Model with most support
*P < 0.05
**P < 0.0001

Table 21. Sum of Akaike weights (Σw_i) for each variable, indicating the relative importance of explanatory variables across models for each species where AT = air temperature, RH = relative humidity, EL = elevation, SU = substrate. Because relative humidity was used in only 2 models while all other variables were used in 3, it does not have an equally represented Akaike weight in this table.

Variable	*P. punctatus*	*P. cylindraceus*	*P. virginia*	*P. cinereus*
AT	0.00	0.85	0.68	0.15
RH	0.00	0.85	0.56	0.12
EL	1.00	1.00	0.30	0.94
SU	0.43	0.90	0.34	0.35

Table 22. Sources and numbers of presence sites for each species, and number of training sites in used in Maxent models with only one presence point per cell.

Species	**Marshall**[1]	**USNM**[2]	**2008**[3]	**Total**	**Training**[4]
P. punctatus	66	59	23	**148**	**54**
P. virginia	17	57	33	**107**	**69**
P. cinereus	34	171	22	**227**	**200**
P. cylindraceus	23	170	38	**231**	**186**

[1] Marshall University Herpetological Museum (West Virginia Biological Survey)
[2] Division of Amphibians and Reptiles, National Museum of Natural History
[3] Sites surveyed from March-November 2008
[4] Sites used when only one site per $1km^2$ is used for training

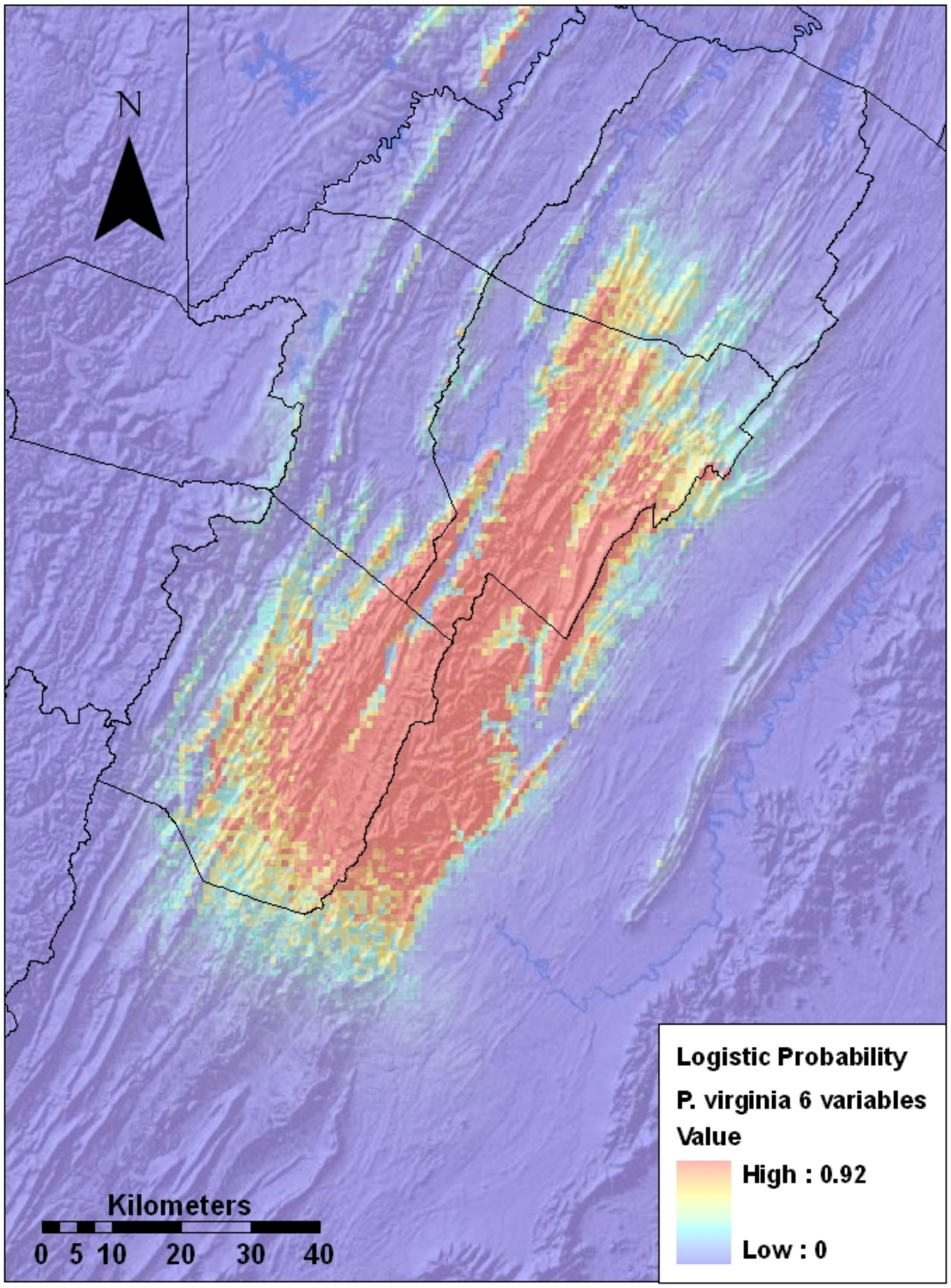


Figure 29. *Plethodon virginia* species distribution model.

Table 23. Six variables used in final species distribution model for *Plethodon virginia* and percent contribution to the gain of the model.

Variable	**Percent contribution**
Mean temp warmest quarter	32.3
Precipitation wettest month	30.2
Temp seasonality	19.9
Annual mean temp	8.2
Precipitation coldest quarter	7.1
Min temp coldest month	2.4

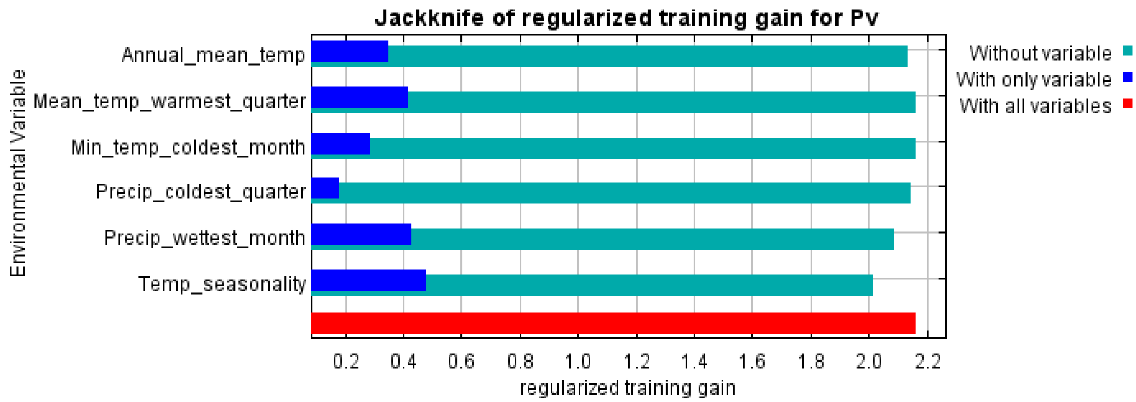


Figure 30. Jackknife results depicting the relative importance of each variable from *Plethodon virginia* distribution models run with each variable as the only variable in the model, and models run without one variable.

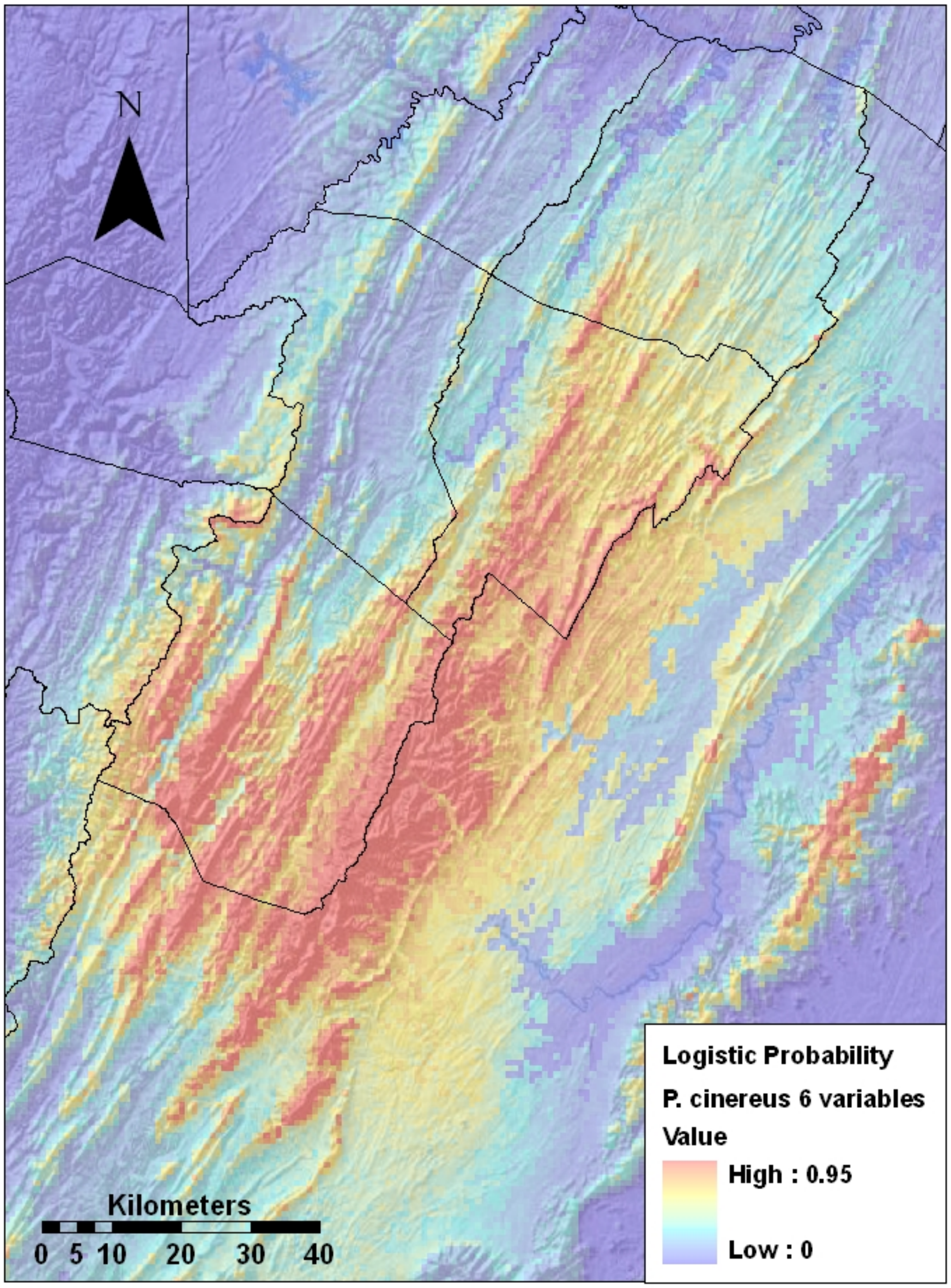


Figure 31. *Plethodon cinereus* species distribution model.

Table 24. Six variables used in final species distribution model for *Plethodon cinereus* and percent contribution to the gain of the model.

Variable	**Percent contribution**
Precipitation wettest month	28.0
Max temp warmest month	25.4
Temp annual range	22.0
Temp seasonality	16.2
Mean temp driest quarter	7.3
Mean temp warmest quarter	1.2

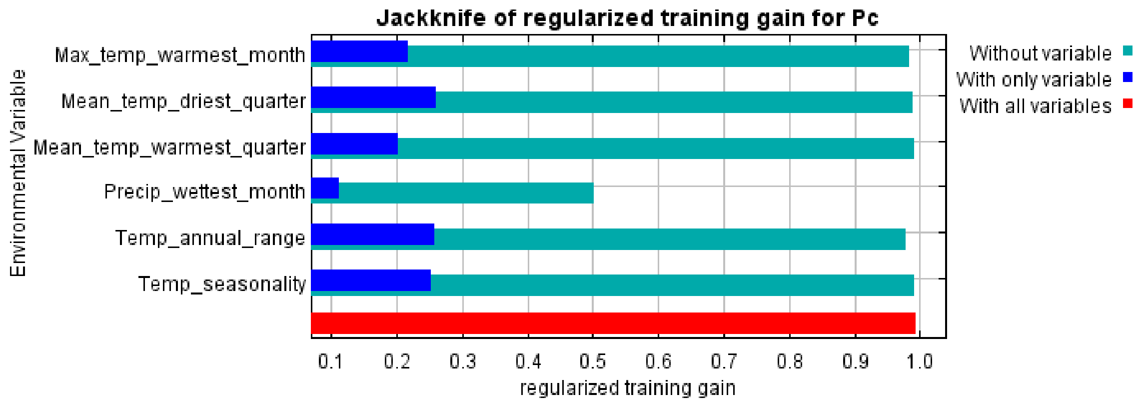


Figure 32. Jackknife results depicting the relative importance of each variable from *Plethodon cinereus* distribution models run with each variable as the only variable in the model, and models run without one variable.

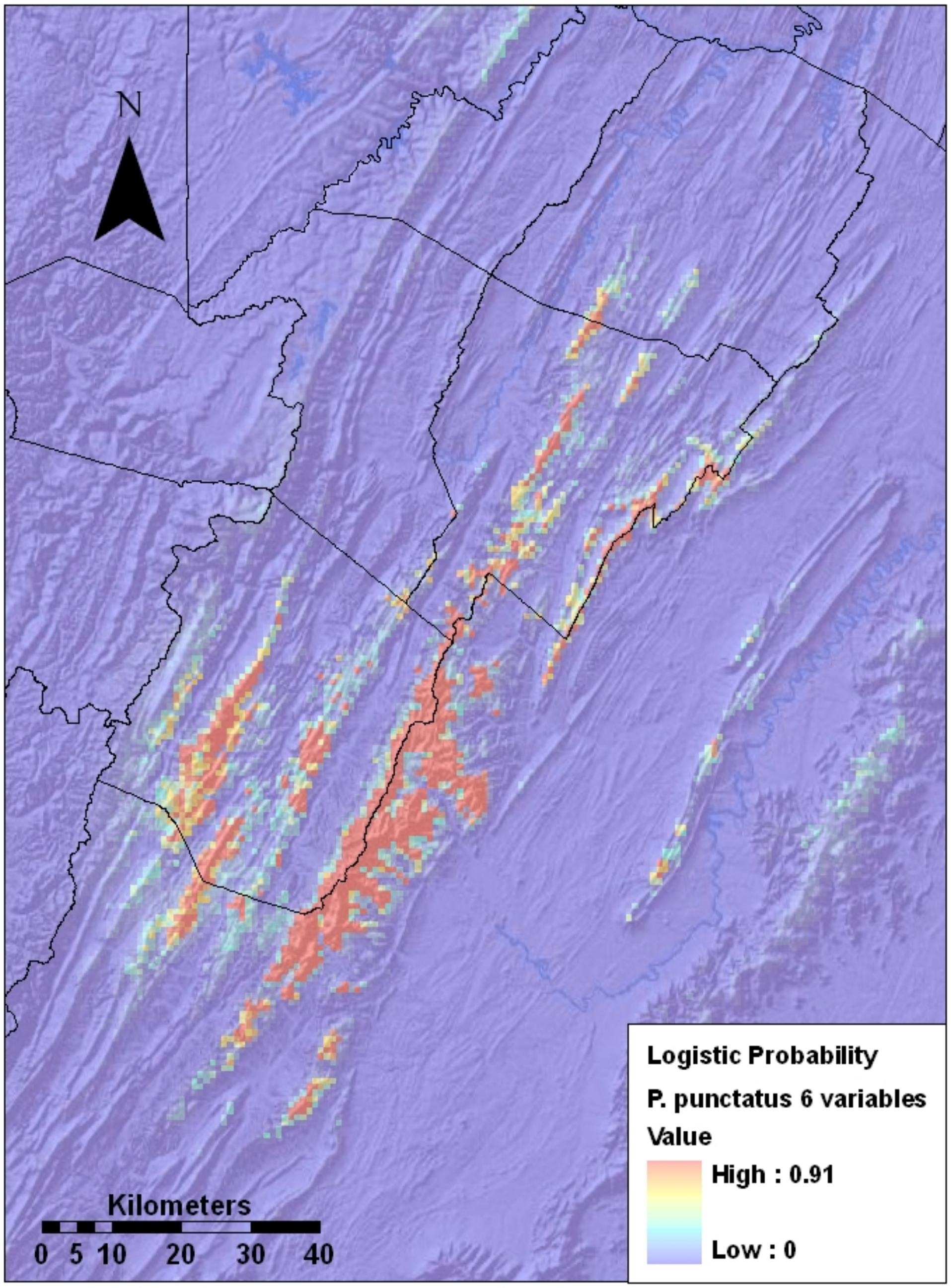


Figure 33. *Plethodon punctatus* species distribution model.

Table 25. Six variables used in final species distribution model for *Plethodon punctatus* and percent contribution to the gain of the model.

Variable	**Percent contribution**
Max temp warmest month	29.9
Precipitation wettest month	29.2
Temp annual range	15.7
Mean diurnal range	11.7
Temp seasonality	9.6
Isothermality	3.9

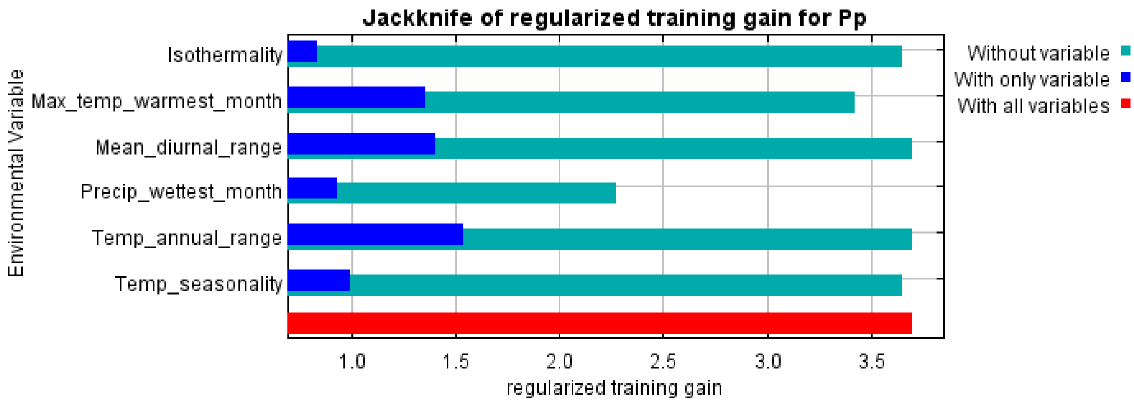


Figure 34. Jackknife results depicting the relative importance of each variable from *Plethodon punctatus* distribution models run with each variable as the only variable in the model, and models run without one variable.

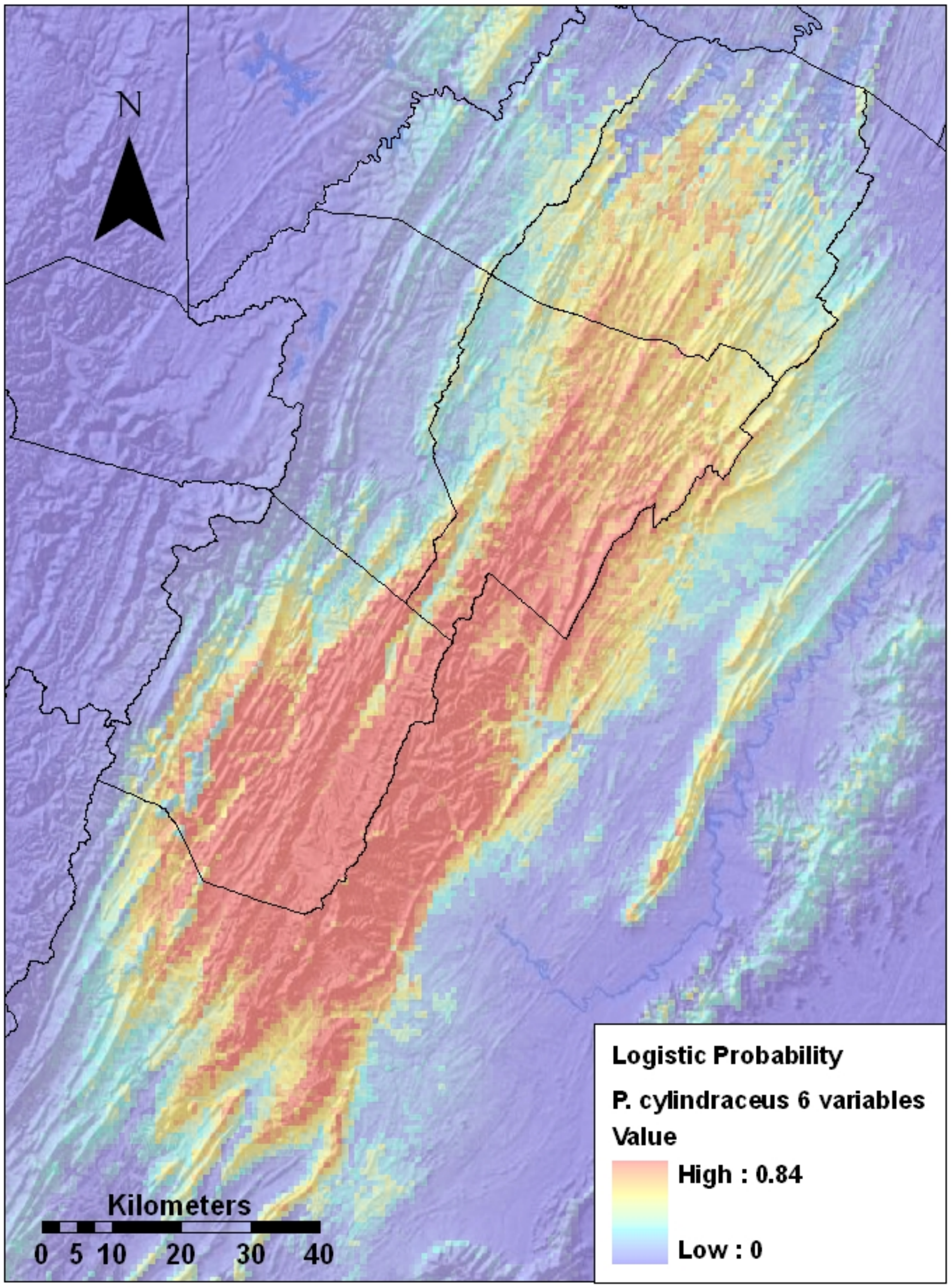


Figure 35. *Plethodon cylindraceus* species distribution model.

Table 26. Six variables used in final species distribution model for *Plethodon cylindraceus* and percent contribution to the gain of the model.

Variable	**Percent contribution**
Precipitation wettest month	27.3
Temp seasonality	19.3
Mean temp driest quarter	17.9
Max temp warmest month	16.6
Precipitation warmest quarter	10.2
Mean temp warmest quarter	8.6

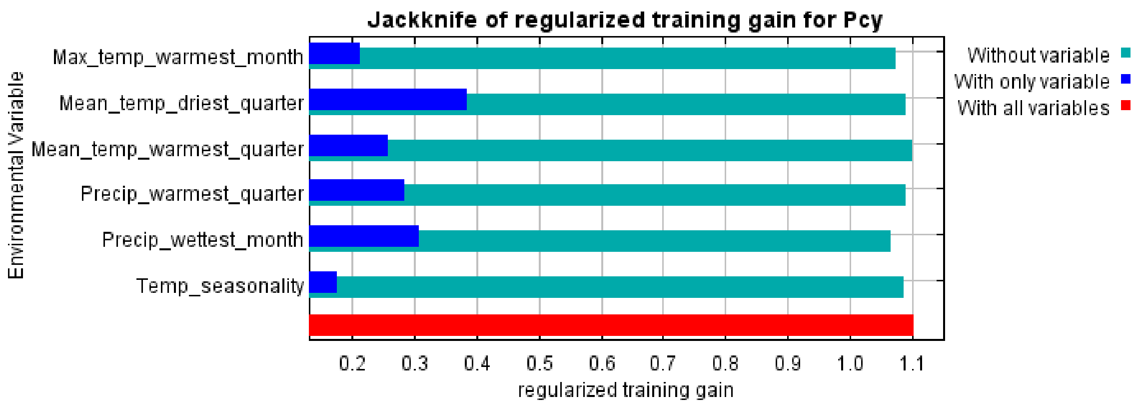
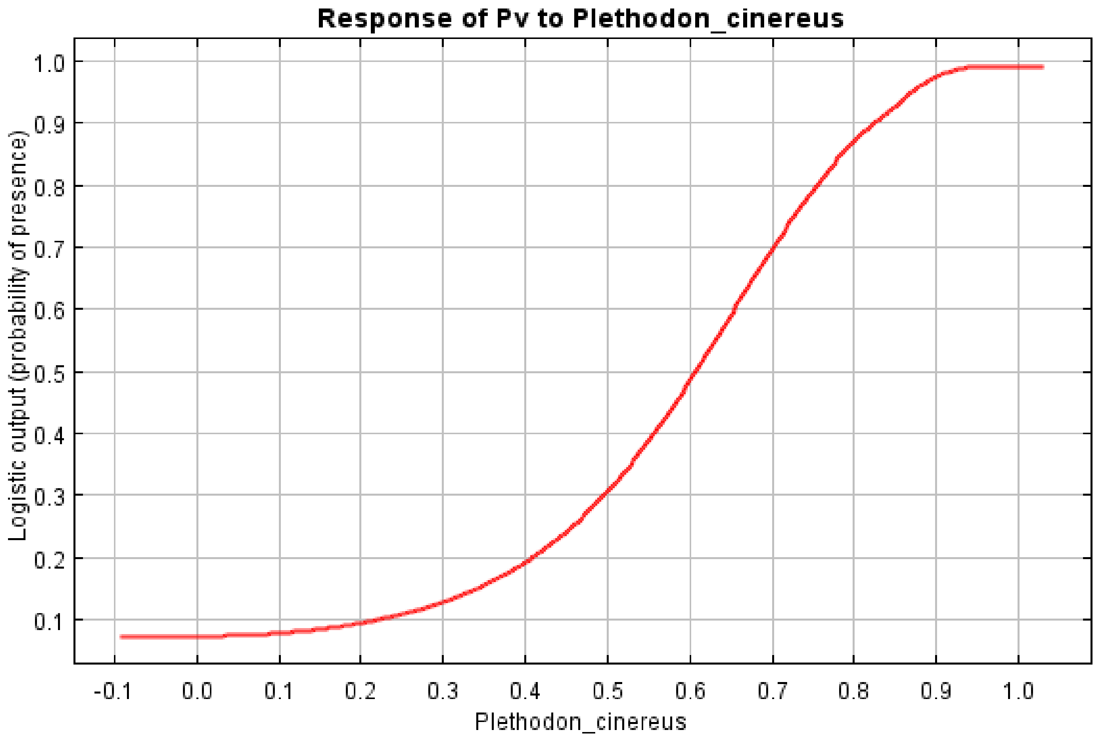


Figure 36. Jackknife results depicting the relative importance of each variable from *Plethodon cylindraceus* distribution models run with each variable as the only variable in the model, and models run without one variable.

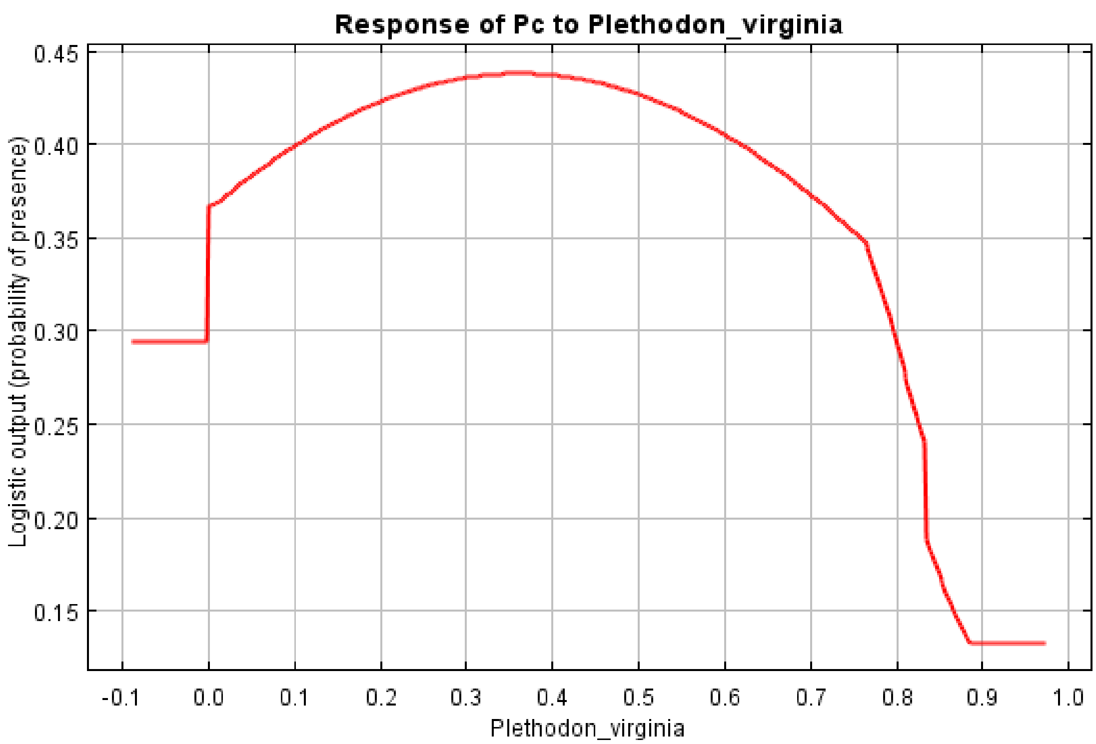
Figure 37. Response curves for *Plethodon virginia* probability of occurrence (A), and *Plethodon cinereus* probability of occurrence (B), when the species distribution model output for the counterpart is used as a seventh variable. The curve represents the change in logistic prediction of occurrence as the environmental variable (in this case, the model of a similar species' modeled probability of occurrence) changes while all other variables (the six environmental variables) remain at their average values from the samples of presence localities.

A



Response of Pv to Plethodon_cinereus
Logistic output (probability of presence)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
-0.1
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Plethodon_cinereus

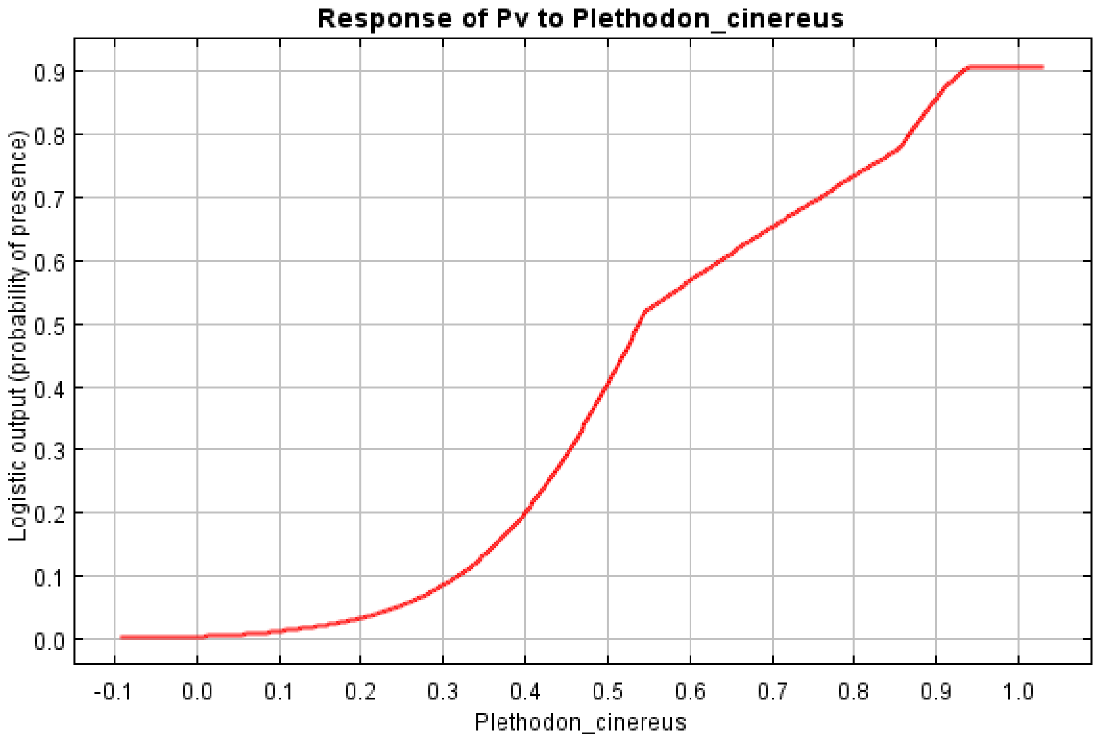
B



Response of Pc to Plethodon_virginia
Logistic output (probability of presence)
0.45
0.40
0.35
0.30
0.25
0.20
0.15
-0.1
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Plethodon_virginia

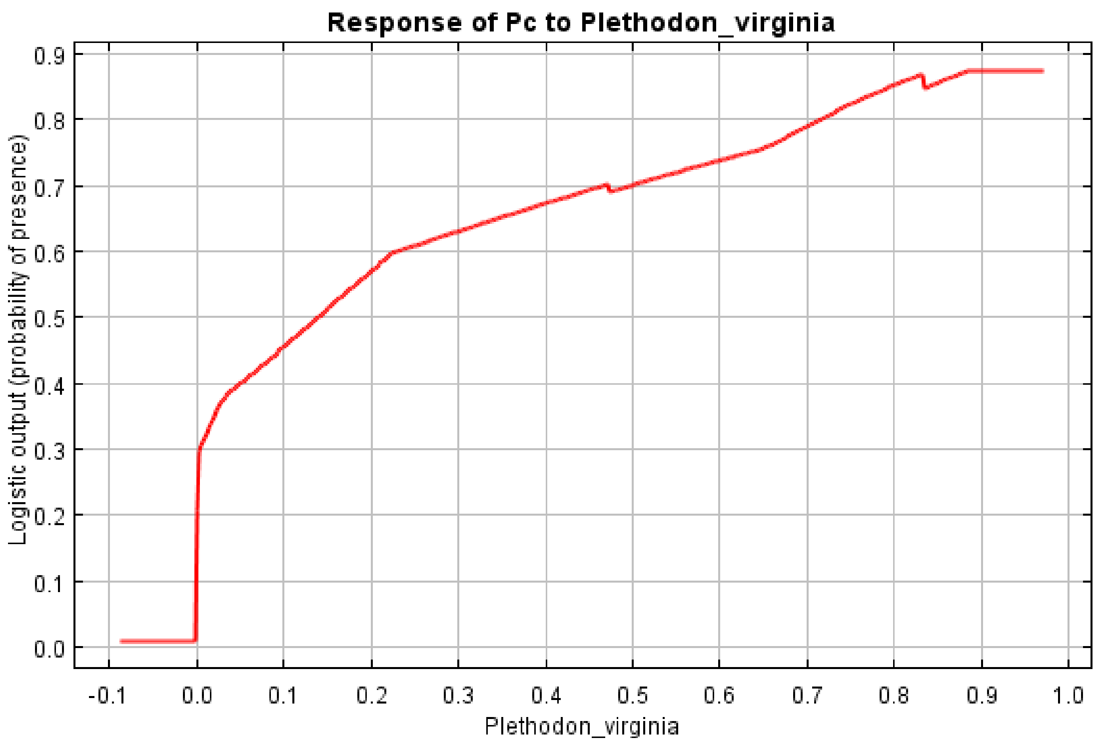
Figure 38. Response curves for *Plethodon virginia* probability of occurrence (A) and *Plethodon cinereus* probability of occurrence (B) when the species distribution model output for the counterpart is used as the sole environmental variable. The curve represents the change in logistic prediction of occurrence as the environmental variable (in this case, the model of a similar species' modeled probability of occurrence) changes.

A



Response of Pv to Plethodon_cinereus
Logistic output (probability of presence)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
-0.1
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Plethodon_cinereus

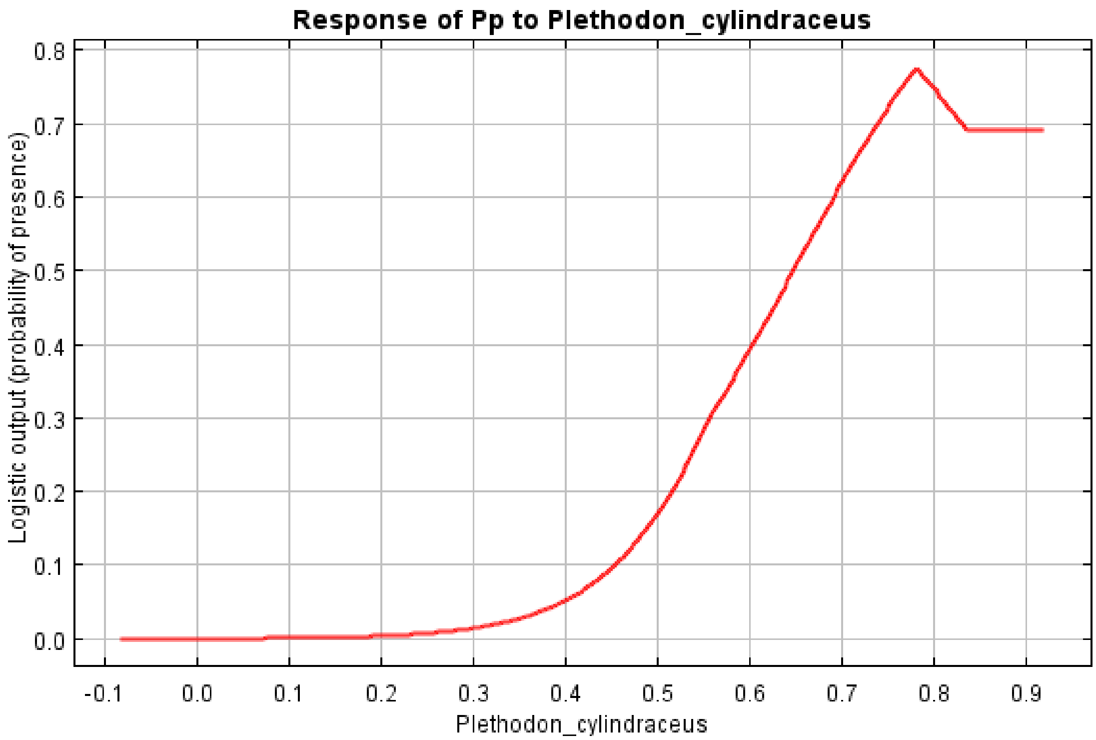
B



Response of Pc to Plethodon_virginia
Logistic output (probability of presence)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
-0.1
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Plethodon_virginia

Figure 39. Response curves for *Plethodon punctatus* probability of occurrence (A) and *Plethodon cylindraceus* probability of occurrence (B) when the species distribution model output for the counterpart is used as a seventh variable. The curve represents the change in logistic prediction of occurrence as the environmental variable (in this case, the model of a similar species' modeled probability of occurrence) changes while all other variables (the six environmental variables) remain at their average values from the samples of presence localities.

A


Response of Pp to Plethodon_cylindraceus
Logistic output (probability of presence)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
-0.1
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Plethodon_cylindraceus

B

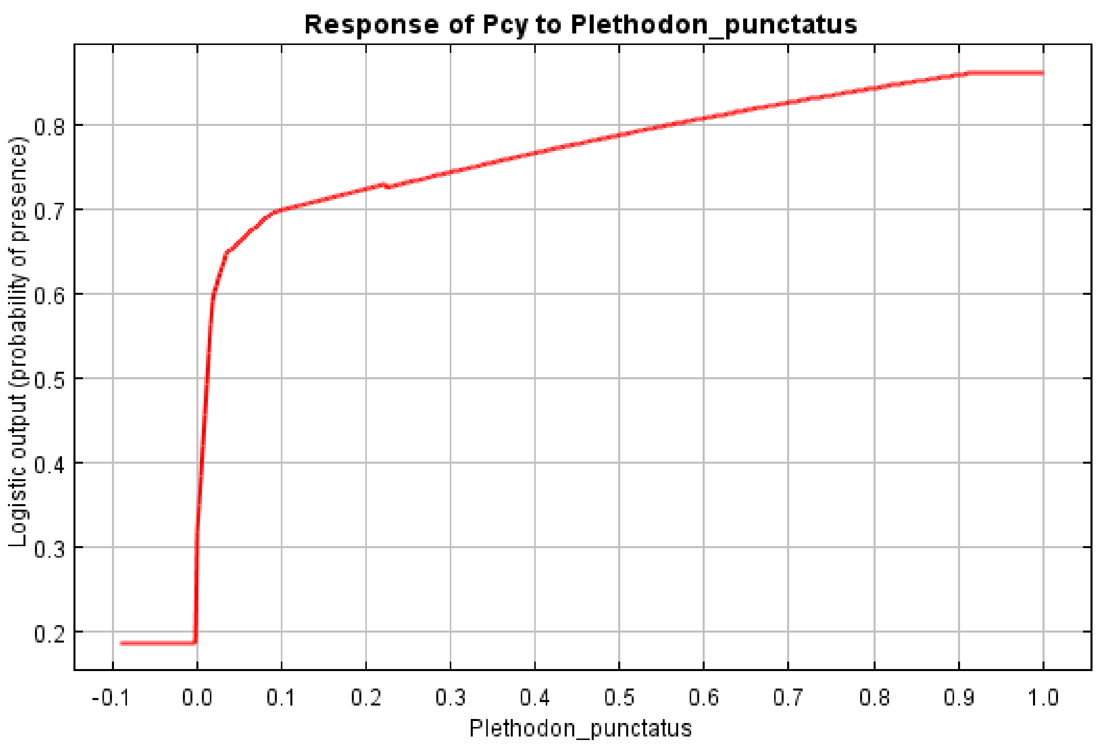
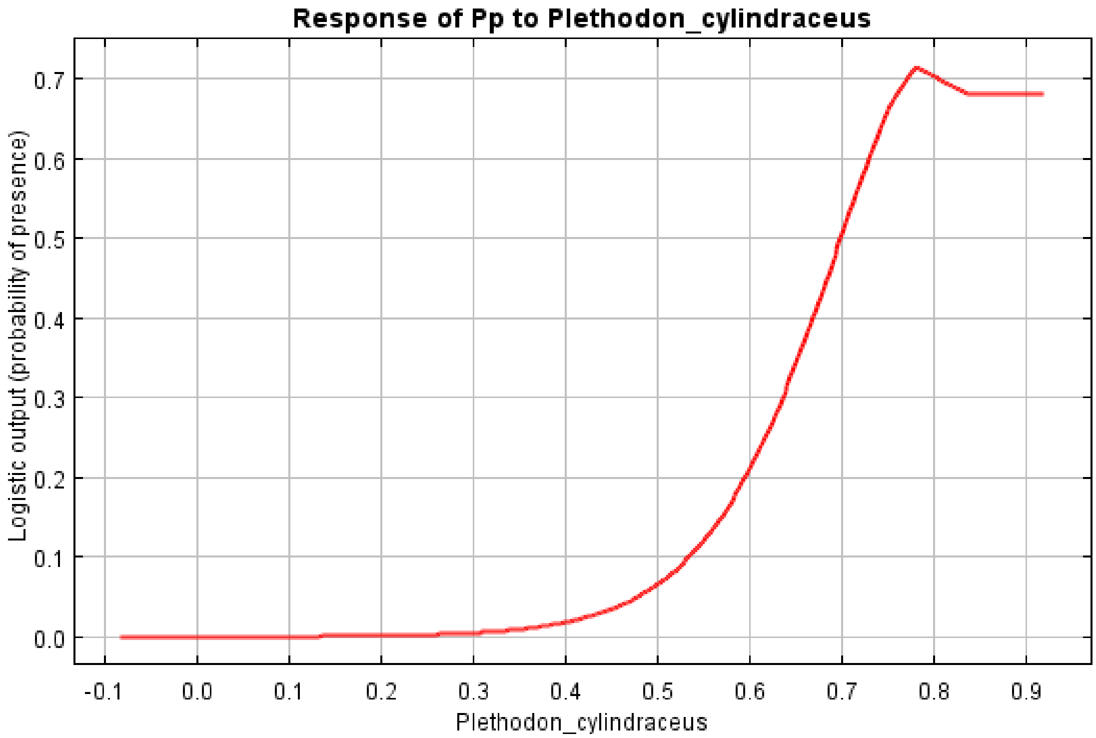
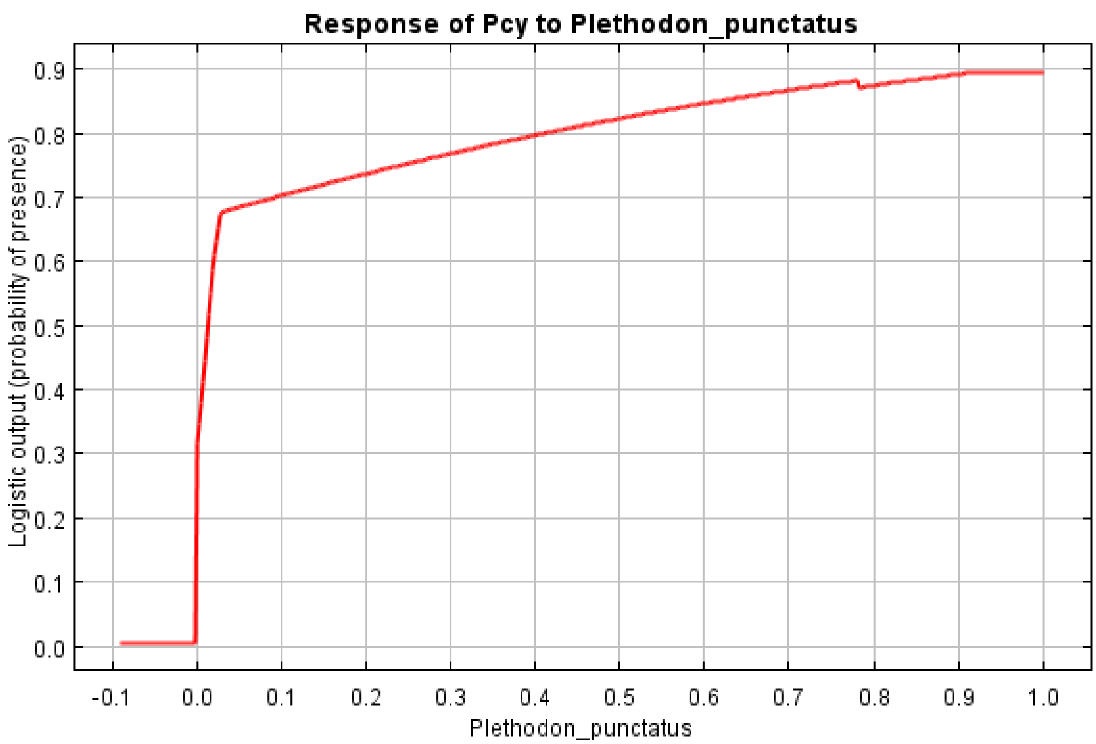

Response of Pcy to Plethodon_punctatus
Logistic output (probability of presence)
0.2
0.3
0.4
0.5
0.6
0.7
0.8
-0.1
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Plethodon_punctatus

Figure 40. Response curves for *Plethodon punctatus* probability of occurrence (A) and *Plethodon cylindraceus* probability of occurrence (B) when the species distribution model output for the counterpart is used as the sole environmental variable. The curve represents the change in logistic prediction of occurrence as the environmental variable (in this case, the model of a similar species' modeled probability of occurrence) changes.

A


Response of Pp to Plethodon_cylindraceus
Logistic output (probability of presence)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
-0.1
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Plethodon_cylindraceus

B


Response of Pcy to Plethodon_punctatus
Logistic output (probability of presence)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
-0.1
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Plethodon_punctatus

Literature Cited

Adams, D. C. and F. J. Rohlf. 2000. Ecological character displacement in *Plethodon*: biomechanical differences found from a geometric morphometric study. Proceedings of the National Academy of Sciences (USA) 97: 4106-4111.

Adams, D. C. 2007. Organization of *Plethodon* salamander communities: guild-based community assembly. Ecology 88: 1292-1299.

Angle, J.P. 1969. The reproductive cycle of the Northern Ravine Salamander, *Plethodon richmondi richmondi*, in the Valley and Ridge Province of Pennsylvania and Maryland. Journal of the Washington Academy of Sciences 59 (7-9): 192-202.

Araujo, M. B. and A. Guisan. 2006. Five (or so) challenges for species distribution modeling. Journal of Biogeography 33: 1677-1688.

Arif, S., D. C. Adam, and J. A. Wicknick. 2007. Bioclimatic modeling, morphology, and behaviour reveal alternative mechanisms regulating the distributions of two parapatric salamander species. Evolutionary Ecology Research 9: 843-854.

Bailey, L. L., T. R. Simons, and K. H. Pollock. 2004. Estimating site occupancy and species detection probability parameters for terrestrial salamanders. Ecological Applications 14 (3): 692-702.

Beamer, D. A. and M. J. Lannoo. 2005. *Plethodon virginia* Highton 1999 species account. Pages 850-852 *in* Amphibian Declines: The Conservation Status of United States Species. University of California Press, Berkeley, CA. 1094 pp.

Bruce R. C. 2009. Intraguild interactions and population regulation in plethodontid salamanders. Herpetological Monographs 22: 31-53.

Buhlmann, K. A., C. A. Pague, J. C. Mitchell, and R. B. Glasgow. Forestry operations and terrestrial salamanders: techniques in a study of the Cow Knob salamander, *Plethodon punctatus*. Pages 38-44 in R.C. Szaro, et al. Management of amphibians, reptiles, and small mammals in North America. USDA For. Serv., Gen. Tech. Rep. RM-166.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, NY, 488 pp.

Conant, R. and J. T. Collins. 1998. Reptiles and amphibians: eastern/central North America. 3rd edition. Houghton Mifflin Company, New York, NY. 616 pp.

Crother, B.I., J. Boundy, J.A. Campbell, K. de Queiroz, R.F. Frost, R. Highton, J.B. Iverson, P.A. Meylan, T.W. Reeder, M.E. Seidel, J.W. Sites Jr. and T.W. Taggart. 2000. Scientific and standard English names of amphibians and reptiles of North America north of Mexico, with comments regarding confidence in our understanding. Herpetological Circular, Number 29, Society for the Study of Amphibians and Reptiles, St. Louis, Missouri.

Crump, M. L. and N. J. Scott. 1994. Visual Encounter Surveys. Pages 84-92 in W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster. Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian Institution Press, Washington, DC.

Cunningham, H. R., L. J. Rissler, and J. J. Apodaca. 2009. Competition at the range boundary in the slimy salamander: using reciprocal transplants for studies on the role of biotic interactions in spatial distributions. Animal Ecology 78: 52-62.

Duellman, W. E. and L. Trueb. 1986. Biology of Amphibians. The Johns Hopkins University Press, Baltimore, MD. 670 pp.

Duellman, W.E. and S.S. Sweet. 1999. Distribution patterns of amphibians in the nearctic region of North America. Pages 31-109 *in* W.E. Duellman, editor. Patterns of distribution of amphibians. Johns Hopkins University Press. Baltimore, Maryland.

Dumas, P. C. 1956. The ecological relations of sympatry in *Plethodon dunni* and *Plethodon vehiculum*. Ecology 37: 484-495.

Dunn, E. R. 1926. The salamanders of the family Plethodontidae. Smith College, Northampton, MA. 441 pp.

Flint, W. D. 2004. Ecology and conservation of the Cow Knob salamander, *Plethodon punctatus*. Unpublished M.S. thesis, James Madison University, Harrisonburg, VA.

Flint, W. D. and R. N. Harris. 2005. The efficacy of visual encounter surveys for population monitoring of *Plethodon punctatus* (Caudata: Plethodontidae). Journal of Herpetology 39: 578-584

Fraser, D. F. 1976*a*. Coexistence of salamanders of the genus *Plethodon*: a variation on the Santa Rosalia theme. Ecology 57: 238-251.

Fraser, D. F. 1976*b*. Empirical evaluation of the hypothesis of food competition in salamanders of the genus *Plethodon*. Ecology 57: 459-471.

Frost, D.R. and D.M. Hillis. 1990. Species in concept and practice: herpetological applications. Herpetologica 46:87–104.

Frost, D. R. 2009. Amphibian Species of the World: an Online Reference. Version 5.3 (12 February, 2009). Electronic Database accessible at http://research.amnh.org/herpetology/amphibia/. American Museum of Natural History, New York, USA.

Graham, M. R. 2007. Distribution and conservation genetics of the Cow Knob salamander, *Plethodon punctatus* Highton (Caudata: Plethodontidae). Unpublished masters thesis, Marshall University, Huntington, WV.

Green, J. 1818. Descriptions of several species of North American Amphibia, accompanied with observations. Journal of the Academy of the Natural Sciences of Philadelphia 1: 348–358.

Green, N. B. and T. K. Pauley. 1987. Amphibians and Reptiles in West Virginia. University of Pittsburgh Press. 241 pp.

Griffis, M. R. and R. G. Jaeger. 1998. Competition leads to an extinction-prone species of salamander: interspecific territoriality in a metapopulation. Ecology 79: 2494-2502.

Grobman, A. B. 1944. The distribution of the salamanders of genus *Plethodon* in eastern United States and Canada. Annals of the New York Academy of Sciences 45: 261-316.

Harlan, R. 1825. Description of a variety of the Coluber fulvius, Linn., a new species of Scincus, and two new species of Salamandra. Journal of the Academy of Natural Sciences of Philadelphia 5: 154–158.

Hairston, N. G. 1949. The local distribution and ecology of the plethodontid salamanders of the southern Appalchians. Ecological Monographs 19: 47-73.

Hairston, N. G. 1951. Interspecies competition and its probable influence upon the vertical distribution of Appalachian salamanders of the genus *Plethodon*. Ecology 32: 266-274.

Hairston, N. G. 1980. The experimental test of an analysis of field distributions: competition in terrestrial salamanders. Ecology 61: 817-826.

Hairston, N. G. 1987. Community Ecology and Salamander Guilds. Cambridge University Press, Cambridge, MA. 230 pp.

Highton, R. 1972. Distribution al interactions among eastern North American salamanders of the genus *Plethodon*. Pages 139-188 *in* P. C. Holt, editor. The distributional history of the biota of the southern Appalachians. Part III: vertebrates. Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.

Highton, R. 1989. Biochemical evolution in the slimy salamanders of the *Plethodon glutinosus* complex in the eastern United States. Part I. Geographic protein variation. Illinois Biological Monographs 57: 1-78.

Highton, R. 1990. Taxonomic treatment of genetically differentiated populations. Herpetologica 46: 114-121.

Highton, R. 1995. Speciation in eastern North American salamanders of the genus *Plethodon*. Annual Review of Ecology and Systematics 26: 579-600.

Highton, R. 1999. Geographic protein variation and speciation in the salamanders of the *Plethodon cinereus* group with the description of two new species. Herpetologica 55: 43-90.

Highton, R. and D. A. Jones. 1965. A striped color phase of *P. richmondi* in Virginia. Copeia 1965: 371-372.

Highton, R. and A. Larson. 1979. The genetic relationships of the salamanders of the genus *Plethodon*. Systematic Zoology 28 (4): 579-599.

Highton, R. and J. R. MacGregor. 1983. *Plethodon kentucki* Mittleman: a valid species of Cumberland Plateau woodland salamander. Herpetologica 39: 189-200

Highton, R. and R. B. Peabody. 2000. Geographic protein variation and speciation in salamanders of the *Plethodon jordani* and *Plethodon glutinosus* complexes in the southern Appalachian Mountains with the description of four new species. Pages 31-93 *in* R. C. Bruce, R.G. Jaeger and L. D. Houck, editors. The biology of plethodontid salamanders. Kluwer Academic/Plenum Publishers, New York, NY, USA.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones and A. Jarvis, 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965-1978.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22: 145-159.

Hyde, E. J. and T. R. Simons. 2001. Sampling plethodontid salamanders: sources of variability. Journal of Wildlife Management 65 (4): 624-632.

Hyde, E. J. and T. R. Simons. 2005. Monitoring salamander populations in the Great Smokey Mountains National Park. Pages 300-306 *in* M. J. Lannoo, editor. Amphibian declines: status of United States species. University of California Press, Berkeley, CA. 1094 pp.

Jaeger, R. G. 1970. Potential extinction through competition between two species of terrestrial salamanders. Evolution 24 (3): 632-642.

Jaeger, R. G. 1971. Competitive exclusion as a factor influencing the distributions of two species of terrestrial salamanders. Ecology 52 (4): 632-637.

Jaeger, R. G. 1980. Density-dependent and density-independent causes of extinction of a salamander population. Evolution 34 (4): 617-621.

Jaeger, R. G. 1981. Dear enemy recognition and the costs of aggression between salamanders. American Naturalist 117 (6): 962-974.

Jaeger, R. G., E. D. Prosen and D. C. Adams. 2002. Character displacement and aggression in two species of terrestrial salamanders. Copeia 2002: 391-401.

Kozak, K. H. and J. J. Wiens. 2006. Does niche conservatism promote speciation? A case study in North American salamanders. Evolution 60 (12): 2604-2621.

Kozak, K. H., D. W. Weisrock, and A. Larson. 2006. Rapid lineage accumulation in a non-adaptive radiation: phylogenetic analysis of diversification rates in eastern North American woodland salamanders (Plethodontidae: *Plethodon*). Proceedings of the Royal Society B 273: 539-546.

Lannoo, M. J., editor. 2005. Amphibian declines: conservation status of United States species. University of California Press, Berkeley, CA. 1094 pp.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy when detection probabilities are less than one. Ecology 83: 2248-2255.

Marsh, D. M. and N. G. Beckman. 2004. Effects of forest roads on the abundance and activity of terrestrial salamanders. Ecological Applications 14 (6): 1882-1891.

Marvin, G. A. 1998. Interspecific aggression and spatial relationships in the salamanders *Plethodon kentucki* and *Plethodon glutinosus*: evidence of interspecific competition. Canadian Journal of Zoology 76: 94-103.

Mitchell, J. C. and T. K. Pauley. 2005. *Plethodon punctatus* Highton 1972 species account. Pages 834-835 *in* M. J. Lannoo, editor. Amphibian Declines: The Conservation Status of United States Species. University of California Press, Berkeley, CA. 1094 pp.

Nishikawa, K. C. 1985. Competition and the evolution of aggressive behavior in two species of terrestrial salamanders. Evolution 39 (6): 1282-1294.

Nishikawa, K. C. 1987. Interspecific aggressive behaviour in salamanders: species-specific interference or misidentification? Aniimal Behaviour 35: 263-270.

Pauley, T. K. 1978. Moisture as a factor regulating habitat partitioning between two sympatric *Plethodon* (Amphibia, Urodela, Plethodontidae) species. Journal of Herpetology 12 (4): 491-493.

Pauley, T. K. 1995. Surveys for *Plethodon punctatus* in the George Washington National Forest, West Virginia. Report submitted to the USDA Forest Service.

Pauley, T. K. 1998. Surveys for *Plethodon punctatus* in areas outside of the George Washington National Forest in West Virginia. Report submitted to the USDA Forest Service.

Pauley, T. K. 2008. The Appalachian inferno: historical causes for the disjunct distribution of *Plethodon nettingi* (Cheat Mountain Salamander). Northeastern Naturalist 15 (4): 595-606.

Petranka, J. W, M. E. Eldridge, and K. E. Haley. 1993. Effects of timber harvesting on southern Appalachian salamanders. Conservation Biology 7 (2): 363-370.

Petranka, J. W. 1998. Salamanders of the United States and Canada. Smithsonian Institute Press, Washington, D.C. 587 pp.

Phillips, S. J., M. Dudik, and R. E. Schapire. 2004. A maximum entropy approach to species distribution modeling. Proceedings of the Twenty-first International Conference on Machine Learning, pp. 655-662.

Soberon, J. and A. T. Peterson. 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. Biodiversity Informatics 2: 1-10.

Strausbaugh, P.D. and E.L. Core. 1978. Flora of West Virginia. Seneca Books, Inc., Grantsville, West Virginia. 1079 pp.

Tucker, R. B. 1998. Ecology and natural history of the Cow Knob salamander, *Plethodon punctatus* Highton, in West Virginia. Unpublished M.S. thesis, Marshall University, Huntington, WV.

Wells, K. D. 2007. The ecology and behavior of amphibians. University of Chicago Press, Chicago, IL, 1400 pp.

Weisrock, D. W., K. H. Kozak, and A. Larson. 2005. Phylogenetic analysis of mitochondrial gene flow and itrogression in the salamander, *Plethodon shermani*. Molecular Ecology 14: 1457-1472.

Welsh, H. H. and S. Droege. A case for using plethodontid salamanders for monitoring biodiversity and ecosystem integrity of North American forests. Conservation Biology 15 (3): 558-569.

Wiens, J. J., T. N. Engstrom, and P. T. Chippindale. 2006. Rapid diversification, incomplete isolation, and the "speciation clock" in North American salamanders (genus *Plethodon*): testing the hybrid swarm hypothesis of rapid radiation. Evolution 60 (12): 2585-2603.

Wyman, R. L. 2003. Conservation of terrestrial salamanders with direct development. Pages 37-52 *in* R. D. Semlitsch (editor), Amphibian Conservation. Smithsonian Press, Washington, D.C. 324 pp.